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Review of the millipede genus *Eutrichodesmus* Silvestri, 1910 (Diplopoda, Polydesmida, Haplodesmidae), with descriptions of new species

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Abstract

Eutrichodesmus, the largest genus in the Oriental family Haplodesmidae, is reviewed and shown to encompass 24 recognizable species, all keyed, including the following nine new species: *E. regularis* **sp. n.**, *E. aster* **sp. n.**, *E. filisetiger* **sp. n.**, *E. curticornis* **sp. n.**, *E. asteroides* **sp. n.** and *E. griseus* **sp. n.** from Vietnam, *E. distinctus* **sp. n.** from China, *E. multilobatus* **sp. n.** from Laos, and *E. reductus* **sp. n.** from Sulawesi, Indonesia. This genus is slightly redefined as follows: Gonopod coxae usually abundantly setose ventrolaterally; telopodite usually slender, not enlarged towards end of femorite, but typically with a more or less distinct process or outgrowth laterally, opposite recurvature point of seminal groove; solenomere thereafter usually comprising most of telopodite, sometimes elaborate; seminal groove normally terminating distally to subapically, with or without a hairpad; acropodite normally small to nearly absent.

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Keywords
Diplopoda, Haplodesmidae, *Eutrichodesmus*, taxonomy, new species, cave, China, Laos, Vietnam, Indonesia

Introduction

The millipede family Haplodesmidae Cook, 1895, which has only six component genera basically occurring (except for a few pantropical introductions) in East and Southeast Asia, as well as the southwestern Pacific region, has recently been reviewed (Golovatch et al. 2009).

The most speciose genus is *Eutrichodesmus* Silvestri, 1910, which contains 15 described species and ranges from southern Japan in the north, through southern China and Indochina, to Vanuatu, Melanesia in the south. The species are as follows (Golovatch et al. 2009):

Eutrichodesmus demangei Silvestri, 1910 (the type species), from Phu-Ly, Hanam Province, North Vietnam (Silvestri 1910);

Eutrichodesmus arcicollaris Zhang *in* Zhang & Wang, 1993, from Huayu Cave, Hekou County, Yunnan, China (Zhang and Wang 1993);

Eutrichodesmus armatocaudatus Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from Hang Lang Lua Cave, Pu Luong, Lung Cao, Thanh Hoa Prov., and a few more caves in and near Cuc Phuong National Park, Ha Nam Ninh Prov., northern Vietnam (Golovatch et al. 2009);

Eutrichodesmus basalis Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from Hang Bo Nau Cave, Dao Bo Hon, Vinh Ha Long Prov., northern Vietnam (Golovatch et al. 2009);

Eutrichodesmus cavernicola (Sinclair, 1901), from Cave Gua Tanan, Raman District and Cave Gua Glap near Biserat, Patani River, Patani District, southern Thailand (Hoffman 1977b);

Eutrichodesmus communicans Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from Vanuatu, Melanesia, southwestern Pacific (Golovatch et al. 2009);

Eutrichodesmus dorsiangulatus (Zhang *in* Zhang & Wang, 1993), from Baoniujiao Cave, Mengla County, Yunnan, China (Zhang, Wang 1993);

Eutrichodesmus gremialis (Hoffman, 1982), from "Chiang Dao caves" in northern Thailand (Hoffman 1982);

Eutrichodesmus incisus Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from caves near Hong Lin, Qianxi County, Guizhou Prov., China (Golovatch et al. 2009);

Eutrichodesmus latus Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from caves in Yachang Nature Reserve, Guangxi Prov., China (Golovatch et al. 2009);

Eutrichodesmus macclurei (Hoffman, 1977), from Batu Caves near Kuala Lumpur, Selangore State, Malaysia (Hoffman 1977a);

Eutrichodesmus monodentus (Zhang *in* Zhang & Wang, 1993), from Caiyun Cave, Mengla County, Yunnan, China (Zhang, Wang 1993);

Eutrichodesmus peculiaris (Murakami, 1966), from two epigean localities in Ehimé Prefecture, Shikoku, Japan (Murakami 1966);

Eutrichodesmus reclinatus (Hoffman, 1977), from Cave Gua Anak Takun at Templer Park near Kuala Lumpur, Selangore State, Malaysia (Hoffman 1977b); and
Eutrichodesmus similis Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009, from two caves in Mulun Nature Reserve, Guangxi Prov., China (Golovatch et al. 2009).

The present paper records another nine new species of *Eutrichodesmus*, thus improving our knowledge of the diversity of this Oriental genus. The descriptions below are arranged by countries in a more or less north-south direction.

Abbreviations used:

MNHN Muséum national d'Histoire naturelle, Paris, France
MZB Museum Zoologicum Bogoriense, Cibinong, Indonesia
SCAU South China Agricultural University, Guangzhou, China
SEM Scanning electron microscopy
ZMUM Zoological Museum, State University of Moscow, Moscow, Russia

Material and methods

The material serving as the basis for the present contribution derives mainly from subterranean collections made in Vietnam, China, Laos, and Indonesia by Anne Bedos and Louis Deharveng (MNHN). The bulk of this material, including most of the holotypes, has been deposited in MNHN, with two holotypes and a few paratypes from China and Indonesia shared between the collections of SCAU and MZB, respectively, and some further paratypes deposited in the collection of ZMUM, as indicated hereafter. The terms "doratodesmid" or "haplodesmid" are used hereafter only in their vernacular meaning, in order to concisely characterize a body shape, i.e. capable or nearly capable of volvation in the former informal group versus vermiform and definitely incapable of valvation in the latter.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope. After examination, SEM material was removed from stubs and returned to alcohol, all such samples being kept at MNHN.

Systematics

***Eutrichodesmus distinctus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:5E777CD8-34D0-4820-9D76-0017195D53AD
Figs 1-3

Type material: China, Guangxi Prov., Fushui, Bapen, Cave 4, 4.III.2005, leg. L. Deharveng and A. Bedos (CHIgx05-035), holotype ♂ (SCAU), paratypes: 1 ♀ (SCAU), 1 ♂ (MNHN JC 317), 1 ♂ (ZMUM), 1 ♂ (SEM).

Name: To emphasize the obvious distinctions from *E. latus* and *E. similis*, these being the only congeners hitherto known from Guangxi Province (Golovatch et al. 2009).

Diagnosis: Differs from all other congeners in the especially distinct metatergal tuberculation, coupled with the lack of tergal trichome, as well as only a few minor details of gonopod structure (in particular, the shape of the telopodite). In addition, it can be separated from the other species known from the same province, *E. latus* and *E. similis*, by the apparently perfect volvation (due to much shorter and more strongly declivous paraterga).

Description: Length of adults of both sexes ca 8.0-8.5 mm, width 1.35–1.40 mm, body broadest at segment 3 or 4. Holotype ca 8.0 mm long and 1.4 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 1).

Adults with 20 segments, body subcylindrical (Figs 1, 2A), conglobation complete, pattern of volvation typical, starting from segment 5 (cf. Golovatch 2003) (Fig. 2B). Head (Fig. 3C) slightly transverse (wider than high), rather densely pilose, microgranular and microvillose just below antennae and on vertex, with a pair of rounded,

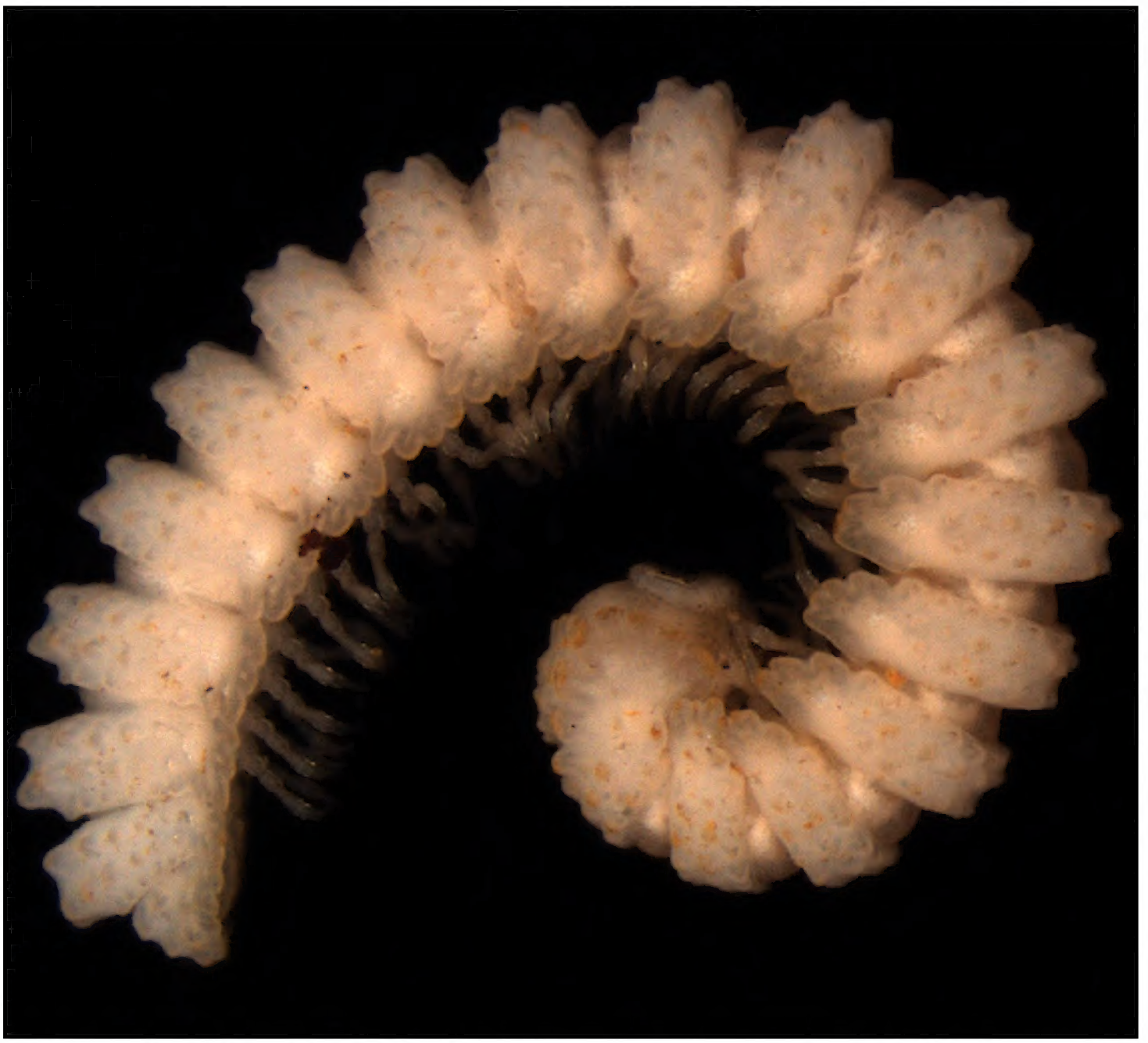


Figure 1. *Eutrichodesmus distinctus* sp. n., ♂ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

paramedian knobs; isthmus between antennal sockets about as wide as diameter of antennal socket. Antennae (Fig. 3C) rather long and slender; antennomere 6 longer than 5, both with an evident dorso-apical pit containing a tight group of minute bacilliform sensilla; antennomere 8 with the usual four sensory cones apically. Collum rather large, broader than head, distinctly flattened medially near front margin, not covering the head from above; entire surface microvillose, with several transverse rows of round tubercles (Fig. 2E). Prozona very finely alveolate, collum and metaterga covered with a cerotegumental crust held by abundant microvilli; stricture between pro- and meta-

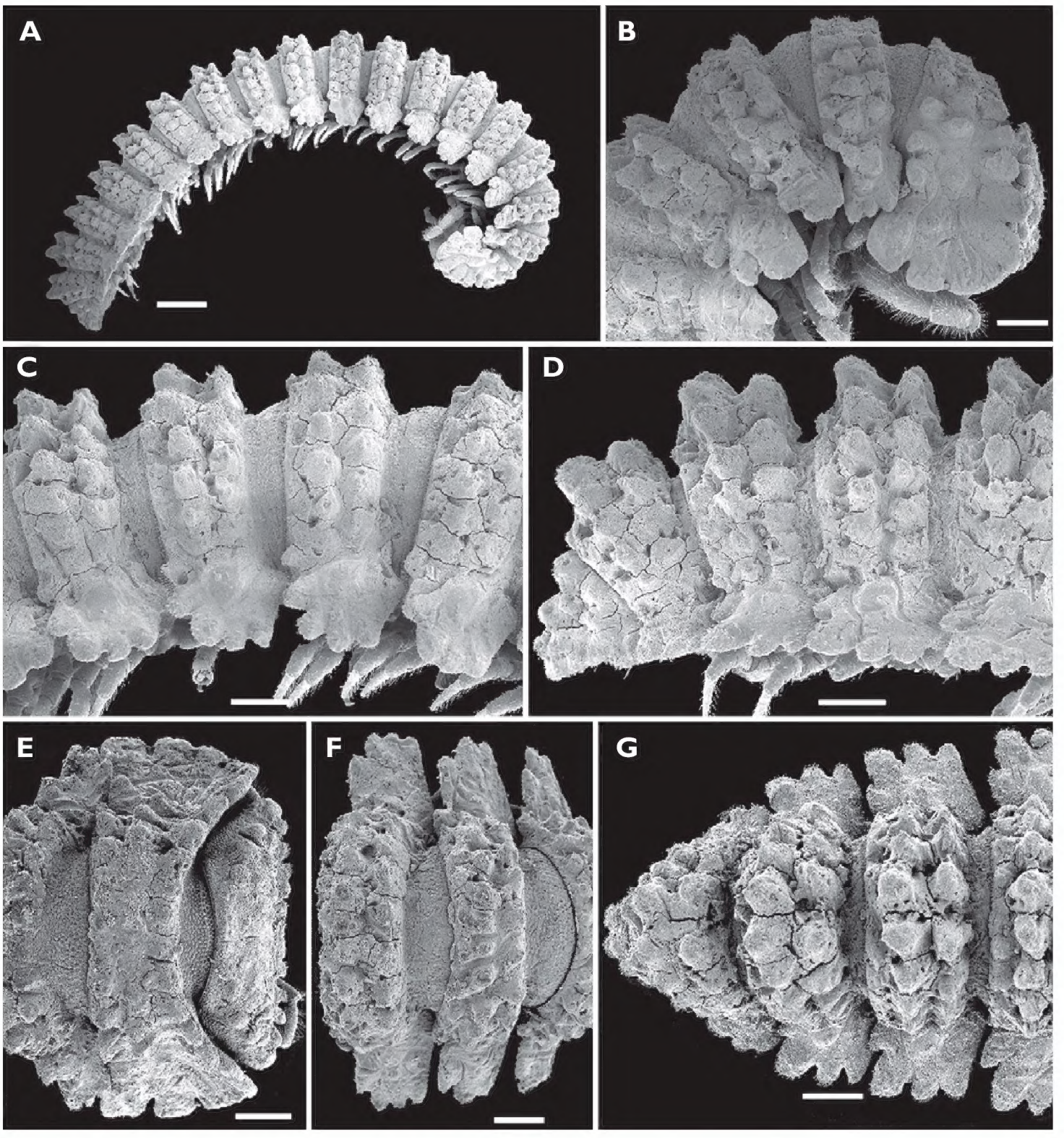


Figure 2. *Eutrichodesmus distinctus* sp. n., ♂ paratype; **A**, habitus, lateral view; **B, E**, anterior part of body, lateral and dorsal views, respectively; **C, F**, midbody segments, lateral and dorsal views, respectively; **D, G**, posterior part of body, lateral and dorsal views, respectively. – Scale bars: A, 0.5 mm; B-G, 0.2 mm.

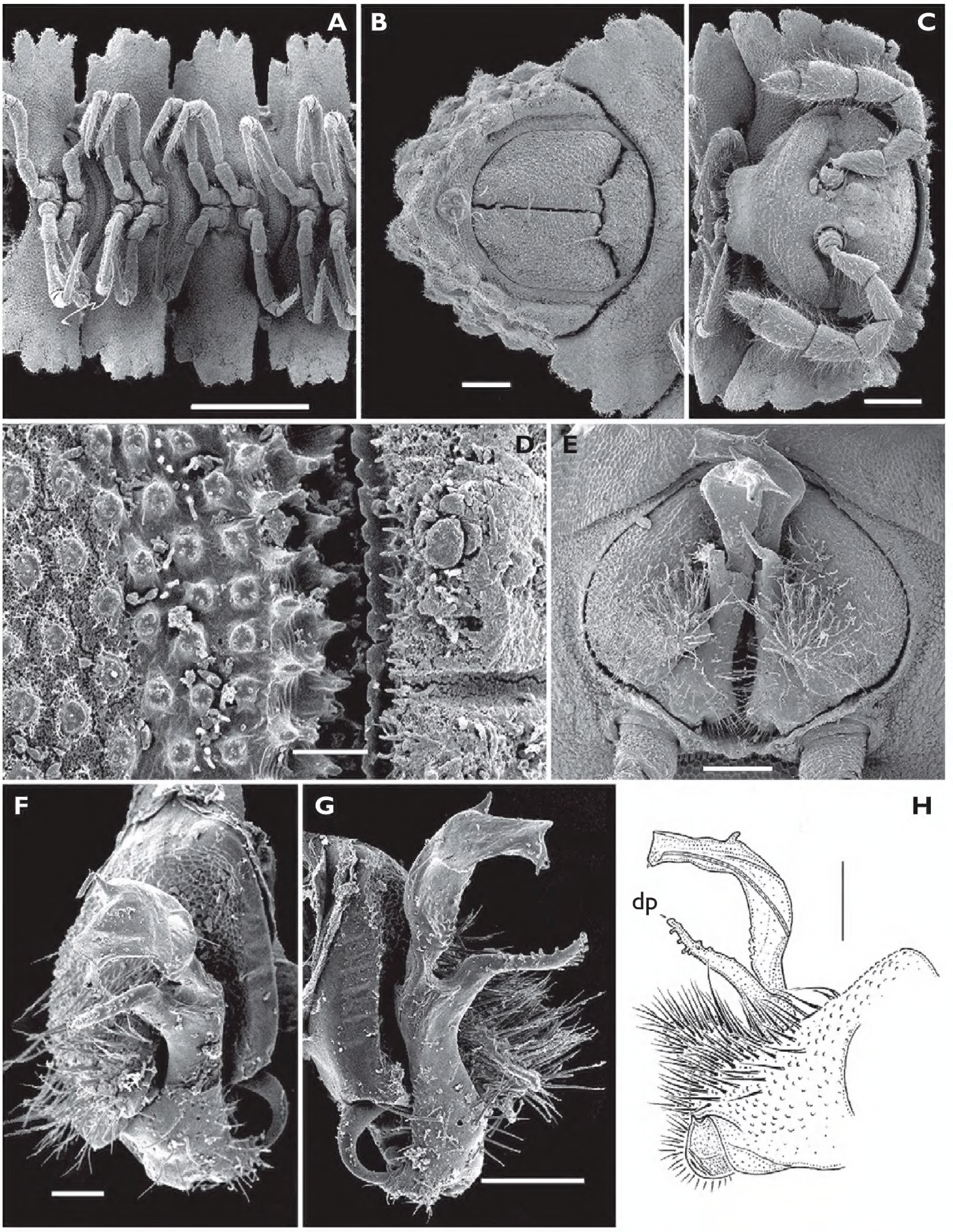


Figure 3. *Eutrichodesmus distinctus* sp. n., ♂ paratypes; **A**, midbody segments, ventral view; **B**, telson, ventral view; **C**, anterior part of body, ventral view; **D**, texture of tegument, dorsal view; **E**, both gonopods *in situ*, ventral view; **F-H**, gonopod, ventral, mesal and lateral views, respectively. – Scale bars: A, 0.5 mm; B, E, G, 0.1 mm; C, H, 0.2 mm; D, 0.02 mm; F, 0.05 mm.

zona broad and shallow, more finely alveolate-microgranular than prozona. Limbus microcrenulate, partly hidden by nearby abundant microvilli (Fig. 3D). Metaterga behind collum with three transverse and mixostictic (i.e. irregular in axial direction) rows of tubercles, second row being highest and best expressed in posterior part of body (Figs 1, 2A-G). Paraterga strongly declivous, rather broad and trilobate laterally, evidently surpassing level of venter, caudolaterally at base with 1-2 distinct lobulations (Figs 2A-G, 3A); middle and, especially, posterior parts of body set off laterally at base by a distinct impression, thus somewhat interrupting contour of convex dorsum; paraterga 2 strongly enlarged, with a series of lobulations anterolaterally, schism and hyposchism both very small; paraterga 3 and 4 slightly shorter than others (Fig. 2B), overlap of following paraterga typical. Pore formula normal (5, 7, 9, 10, 12, 13, 15-19), ozopores very indistinct, located near top of caudolateral lobulation. Metatergal setation wanting. Pleurotergal ridges absent. Epiproct short, also with differentiated tubercles, directed ventrocaudad, with the usual four cones just below tip. Hypoproct and paraprocts normal (Fig. 3B).

Sterna usually with a deep, narrow, transverse depression between coxae (Fig. 3A), only sterna between ♂ coxae 6, 7 and 9 much wider. Gonopod aperture suboval, relatively small, far from reaching lateral sides of segment 7 (Fig. 3E). Legs rather long and relatively slender, barely reaching tips of paraterga; femoral and tarsal segments longest, subequal in length; claw normal, simple, very slightly curved ventrad; some setae with microdenticulations (Fig. 3A).

Gonopods (Figs 3F-H) very simple. Coxae subquadrate, large, microtuberculate and abundantly setose ventrolaterally, with a conspicuous triangular lobe frontolaterally. Telopodite longer than coxite, slender throughout, setose in its basal half, with a conspicuous, denticulate, lateral, distofemoral process (dp) at about midway, seminal groove terminating subapically near a small spiniform prong.

Remarks: This pallid species shows differentiation of the metatergal tubercles in the second row growing steadily higher towards the telson, coupled with the absence of tergal setation. It is a typical "doratodesmid" (capable of volvation, see Golovatch et al. 2009), possibly a troglobite.

***Eutrichodesmus regularis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:5137C5B6-4F58-4BCC-A746-21705E195066
Figs 4-7

Type material: Vietnam, Lao Cai Prov., Sa Pa, Hang Ta Phin Cave, hand collected, 11.VIII.2003, leg. L. Deharveng and Bedos (Vn0308-009), holotype ♂ (MNHN JC 318), paratypes: 1 ♂, 2 ♀, 1 subad., 1 juv. (MNHN JC 318), 1 ♀ (ZMUM), 1 ♂ (SEM).

Name: To emphasize the highly regular, isostictic (i.e. regular rows not only transversely, but also longitudinally) and almost undifferentiated pattern of metatergal tuberculation.

Diagnosis: Differs from congeners by the perfect volvation, coupled with faint metatergal lobulations, the especially regular, nearly undifferentiated and isostictic pattern of metatergal tuberculation, the peculiar, phylloid tergal setae and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Description: Length of adults of both sexes ca 9.0-10.0 mm, width 1.7-1.8 mm, body broadest at segment 3 or 4. Holotype ca 10 mm long and 1.7 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 4).

Adults with 20 segments, pattern of conglobation typical of "doratodesmids" (Figs 4, 5A). Head, antennae (Fig. 5E), tegument (Figs 6A-C), sterna (Fig. 6E), gonopod aperture (Fig. 6F) and many other characters (Figs 5F, 6D) much as in *E. distinctus* sp. n., but collum more regularly tuberculate and slightly flattened mid-dorsally (Fig. 5B). Metater-

Figure 4. *Eutrichodesmus regularis* sp. n., ♂ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

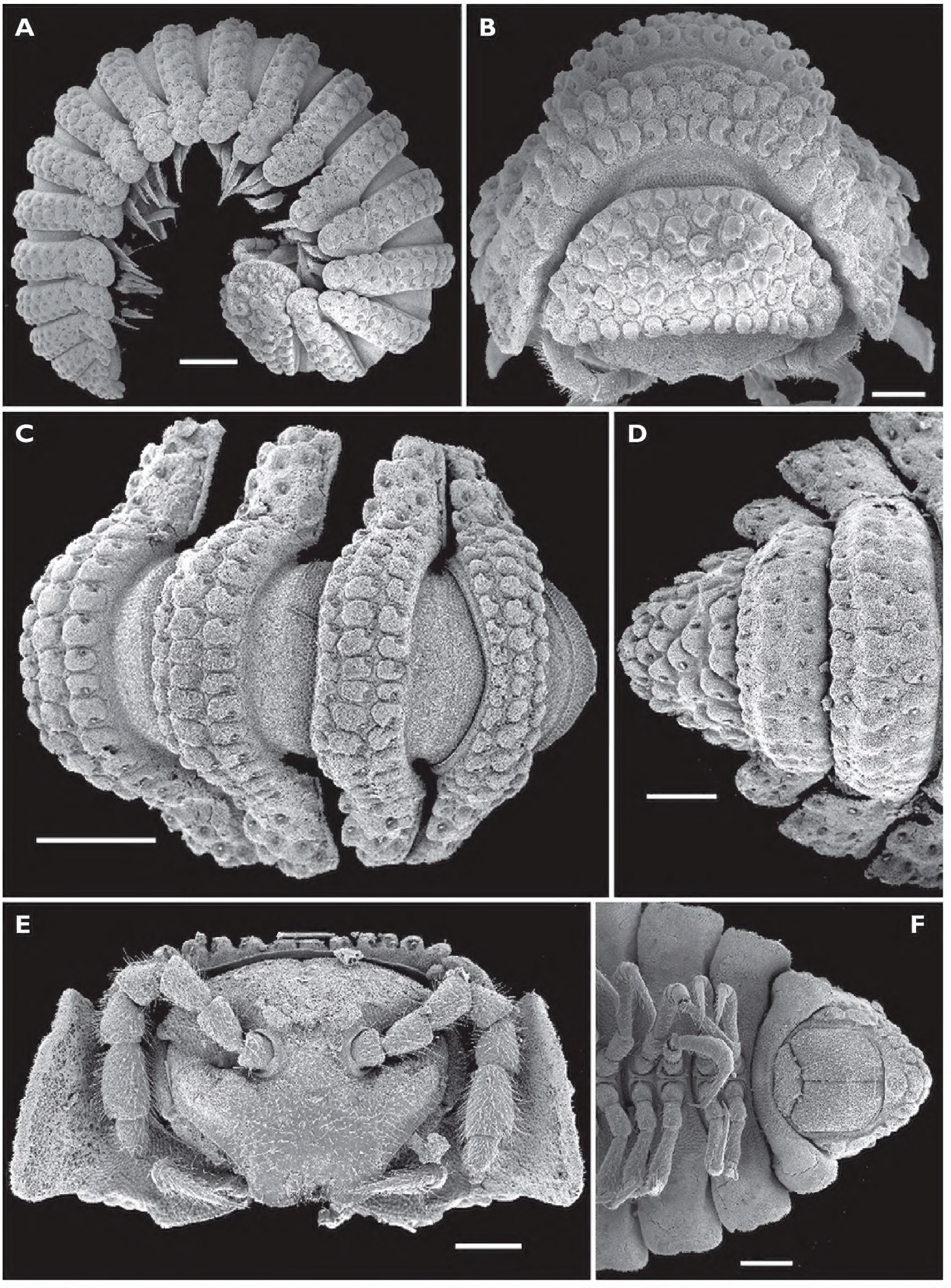


Figure 5. *Eutrichodesmus regularis* sp. n., ♂ paratype; **A**, habitus, lateral view; **B, E**, anterior part of body, frontodorsal and ventral views, respectively; **C**, midbody segments, dorsal view; **D, F**, posterior part of body, dorsal and ventral views, respectively. – Scale bars: A, C, 0.5 mm; B, D-F, 0.2 mm.

ga behind collum with three transverse, very regular and isostictic rows of subequally-sized, rounded, flat, nearly undifferentiated tubercles (Figs 5A-D), each crowned with a short, 2-segmented, phylloid seta (Fig. 6C). Paraterga directed ventrolaterad, rather broad, slightly surpassing level of venter, slightly interrupting general outline of convex dorsum (Figs 5A, C, 6D); paraterga 2 strongly enlarged, each margin nearly entire, with only very faint traces of a series of small lobulations anterolaterally (Figs 4, 5A, B, D). Following paraterga broadly rounded and slightly 3- or 4-lobate laterally and at least distinctly bilobate caudolaterally (Figs 5A, C, D, 6F). Limbus very faintly crenulate, almost

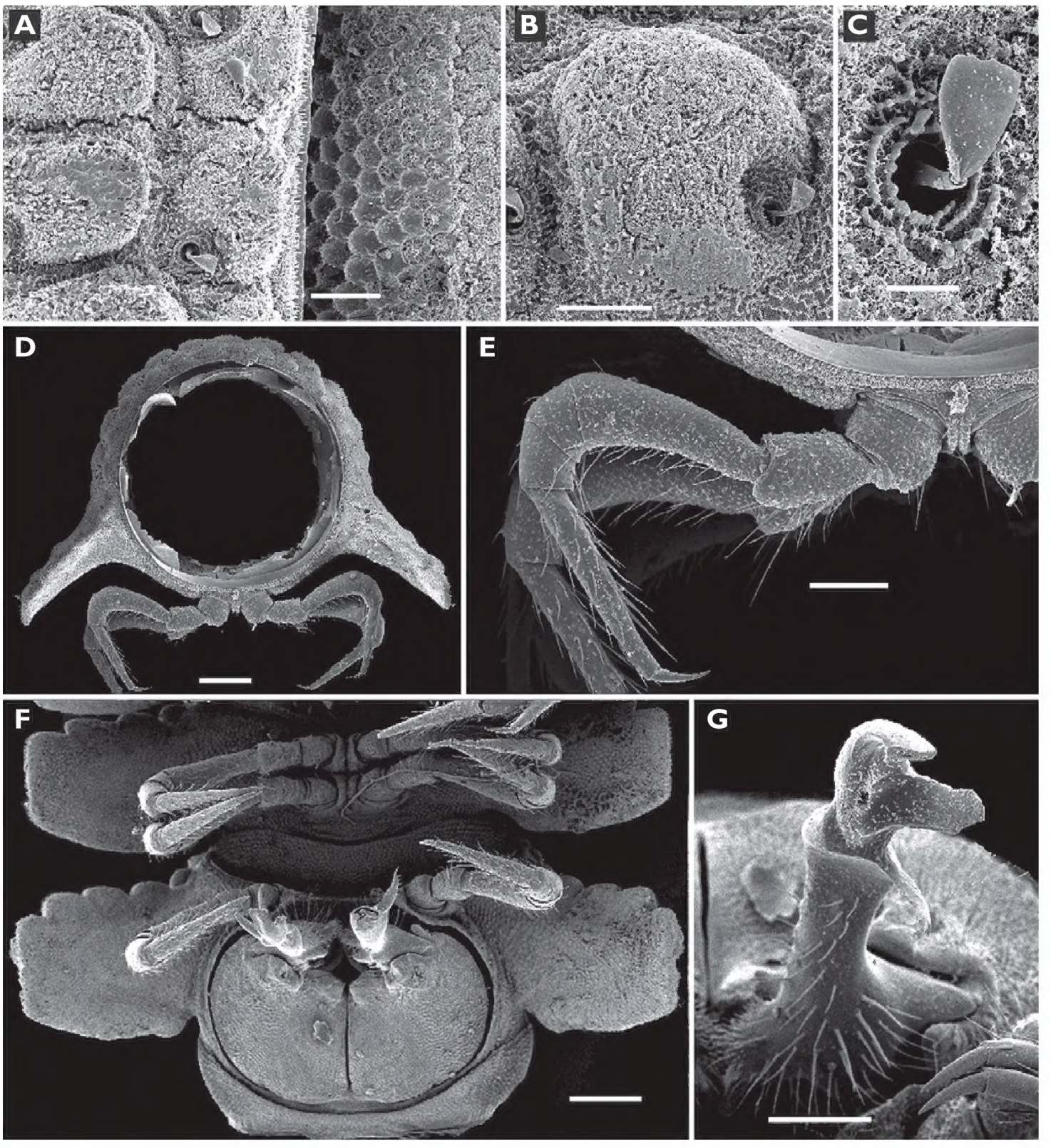


Figure 6. *Eutrichodesmus regularis* sp. n., ♂ paratype; **A**, texture of tegument, dorsal view; **B**, metatergal tubercle, dorsal view; **C**, metatergal seta, dorsal view; **D**, cross-section of a midbody segment, caudal view; **E**, midbody legs, caudal view; **F**, segments 7 and 8, ventral view; **G**, left gonopod *in situ*, caudoventral view. – Scale bars: A, B, 0.05 mm; C, 0.01 mm; D, F, 0.2 mm; E, G, 0.1 mm.

hidden by nearby abundant microvilli (Fig. 6A). Pore formula normal, ozopores poorly visible, located dorsally near tip of ventrocaudal lobulation (Figs 5C, D).

Legs relatively long, slightly surpassing edge of paraterga (Figs 6D, E).

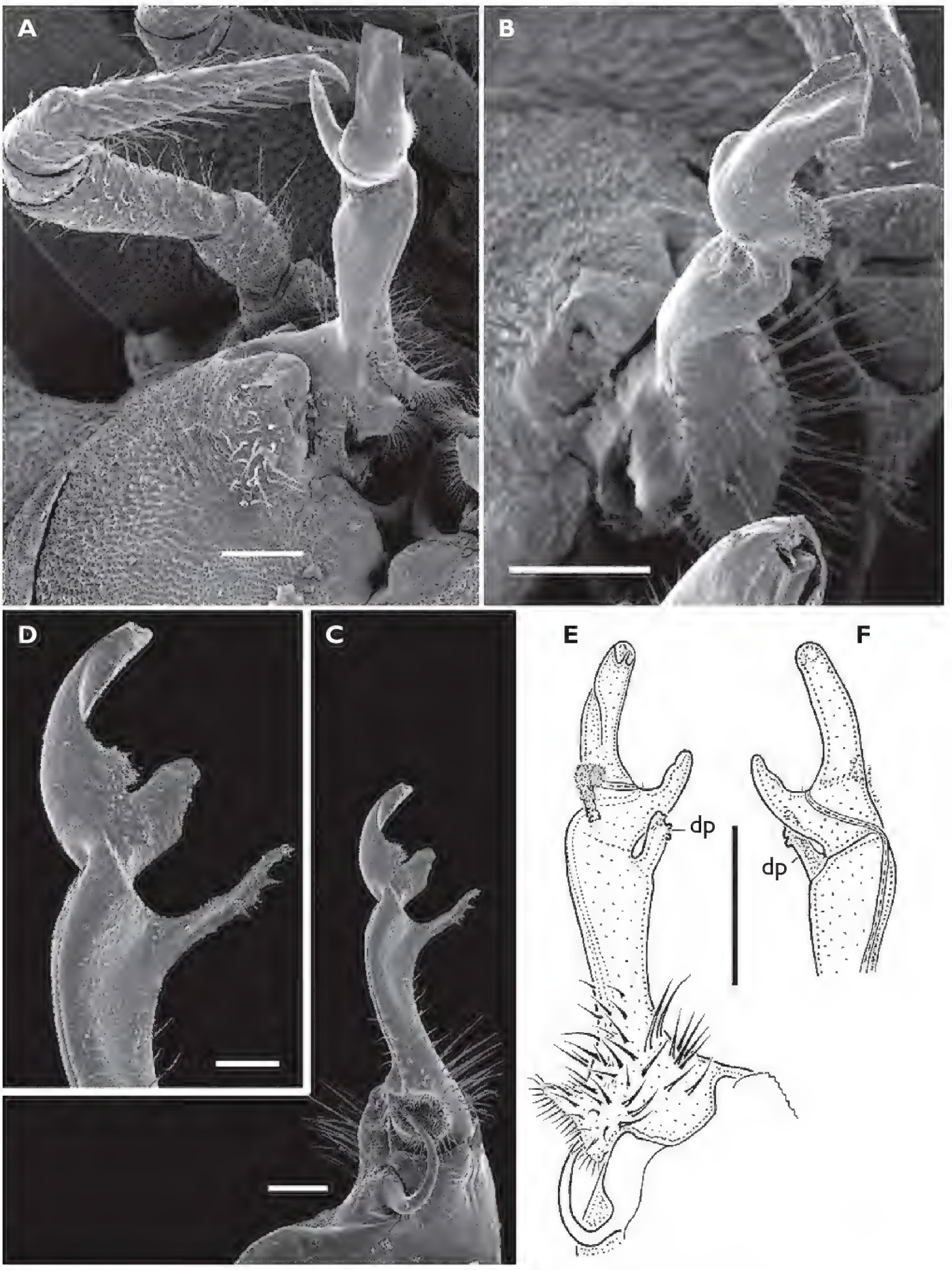


Figure 7. *Eutrichodesmus regularis* sp. n., ♂ paratypes; **A-F**, gonopods, frontoventral, submesal, mesal, mesal and lateral views, respectively. – Scale bars: A-C, 0.1 mm; D, 0.05 mm; E, F, 0.2 mm.

Gonopods (Figs 6F, G, 7A-E) relatively complex. Coxae subquadrate, large, microtuberculate, nearly bare, with only a few, mostly short setae on and near base of a small ventro-apical lobe. Telopodite considerably longer than coxite, slightly stouter and setose in its basal half, with an inconspicuous, digitiform, simple, lateral, distally papillate, distofemoral process (dp) at about midway, more distally with another simple outgrowth with its base marking recurvature point of a relatively short seminal groove; acropodite (= solenomere) relatively stout, lamelliform, slightly curved along main axis, with two small denticles apically and a conspicuous pilose-spinulate pulvillus near base (Figs 7E, F).

Remarks: This pallid species shows highly peculiar, phylloid but very short, tergal setae and undifferentiated metatergal tubercles. It is also a typical "doratodesmid", possibly another troglobite.

Eutrichodesmus aster **Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:B107B0B1-7423-466C-8E47-BE50F0EA0D5D
Figs 8-11

Type material: Vietnam, Yen Bai Prov., Nghia Lo: Xa Som a, Tham Han Cave, hand collected, 20.XII.2003, leg. L. Deharveng, A. Bedos and Phuong (Vn0312-46), holo-

Figure 8. *Eutrichodesmus aster* sp. n., ♂ paratype from Tham Han Cave; habitus, lateral view. (Photographed not to scale by L. Deharveng).

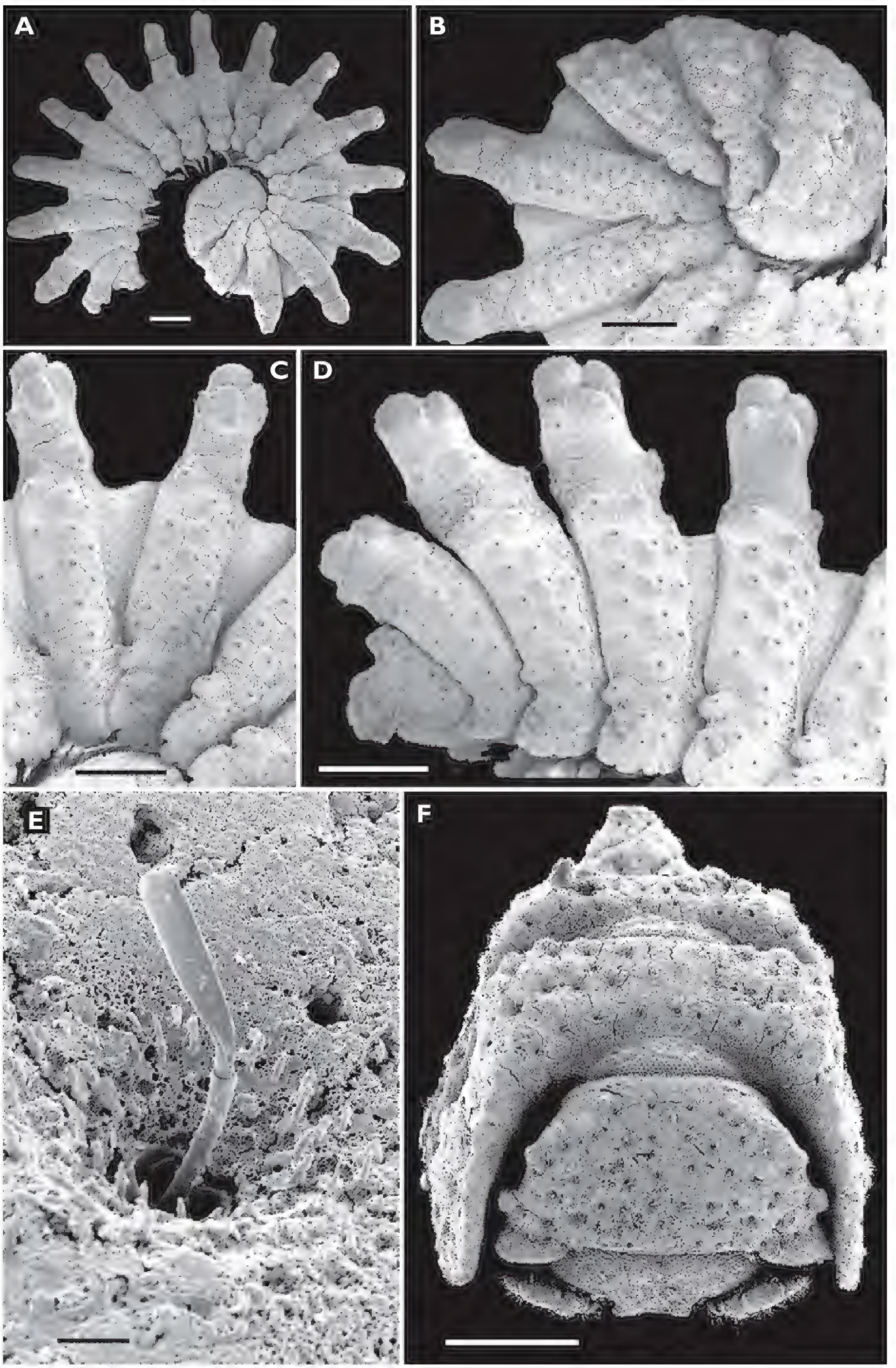


Figure 9. *Eutrichodesmus aster* sp. n., subadult paratype from Tham Han Cave; **A**, habitus, lateral view; **B**, anterior part of body, lateral view; **C**, midbody segments, lateral view; **D**, posterior part of body, lateral view; **E**, metatergal seta, sublateral view; **F**, anterior part of body, frontodorsal view. – Scale bars: A-D, F, 0.5 mm; E, 0.001 mm.

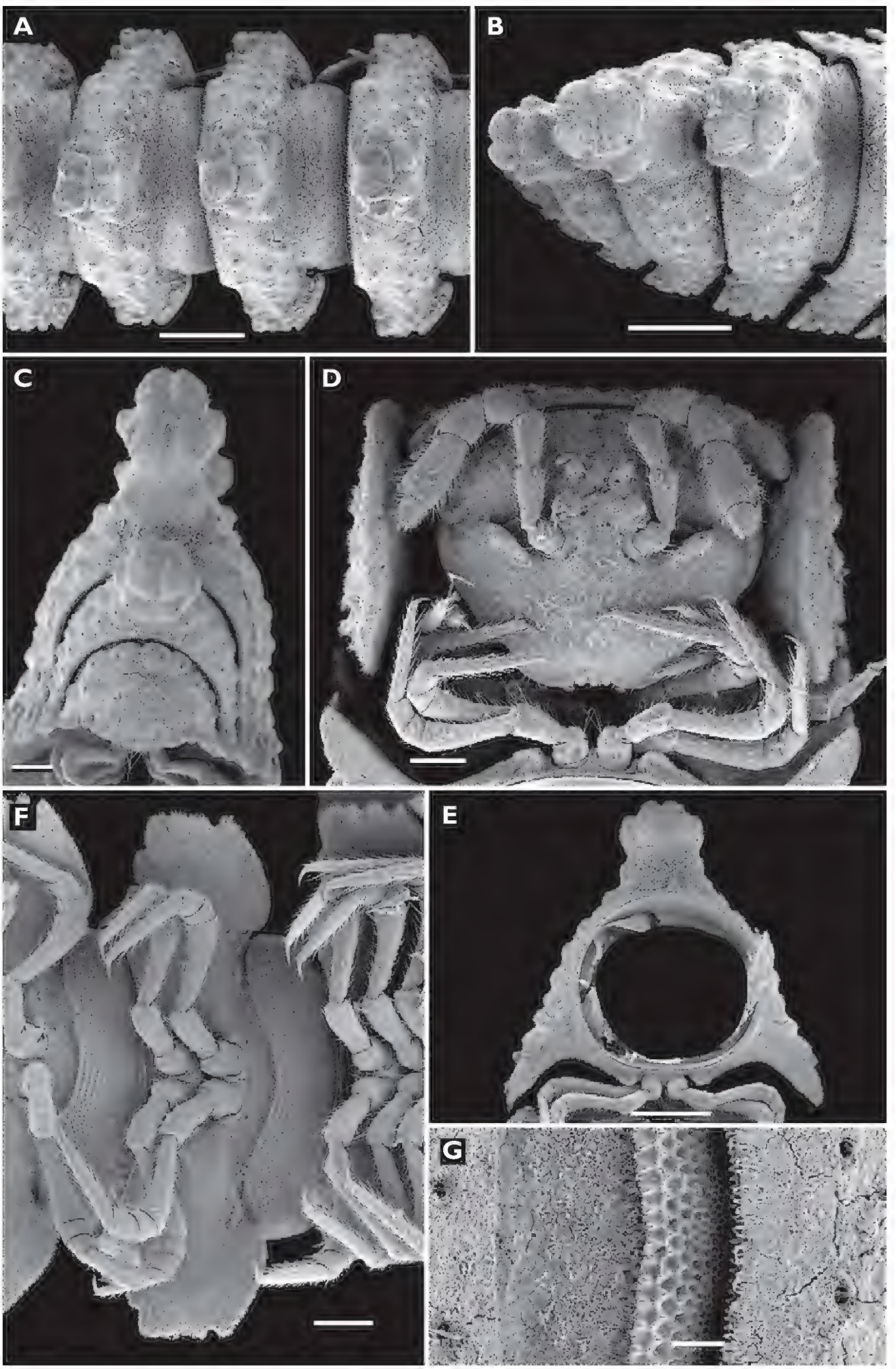


Figure 10. *Eutrichodesmus aster* sp. n., subadult paratype from Tham Han Cave; **A, E**, midbody segments, dorsal and ventral views, respectively; **B, C**, posterior part of body, dorsal and caudal views, respectively; **D**, anterior part of body, ventral view; **F**, cross-section of a midbody segment, caudal view; **G**, texture of tegument, dorsal view. – Scale bars: A, B, F, 0.5 mm; C-E, 0.2 mm; G, 0.05 mm.

type # (MNHN JC 319), paratypes: 1 ♂, 1 ♀, 2 subad., 1 juv. (MNHN JC 319), 1 ♂, 1 subad. (ZMUM), 1 subad. (SEM). Vietnam, Yen Bai Prov., Nghia Lo: Tham Lê Cave, hand collected, 19.XII.2003, leg. L. Deharveng, A. Bedos and Phuong (Vn0312-38), paratypes: 2 ♂ (MNHN JC 319). Vietnam, Yen Bai Prov., Nghia Lo: Hang Dan Khao Cave, hand collected, 20.XII.2003, leg. L. Deharveng, A. Bedos and Phuong (Vn0312-48), 1 ♂ (fragm.), 1 ♀ (MNHN JC 319), 1 ♀, 1 juv. (ZMUM).

Name: To reflect the star-shaped and discoid body of the volvated animal.

Diagnosis: Differs from all congeners, except *E. macclurei* and *E. reclinatus*, by the extremely high mid-dorsal crests on metaterga 5-19. In addition, it can be distinguished from *E. macclurei* and *E. reclinatus* in the presence of a mid-dorsal projection on metatergum 4, the slightly more strongly declivous and quadrilobate paraterga. The new species differs from all other species of the genus in minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

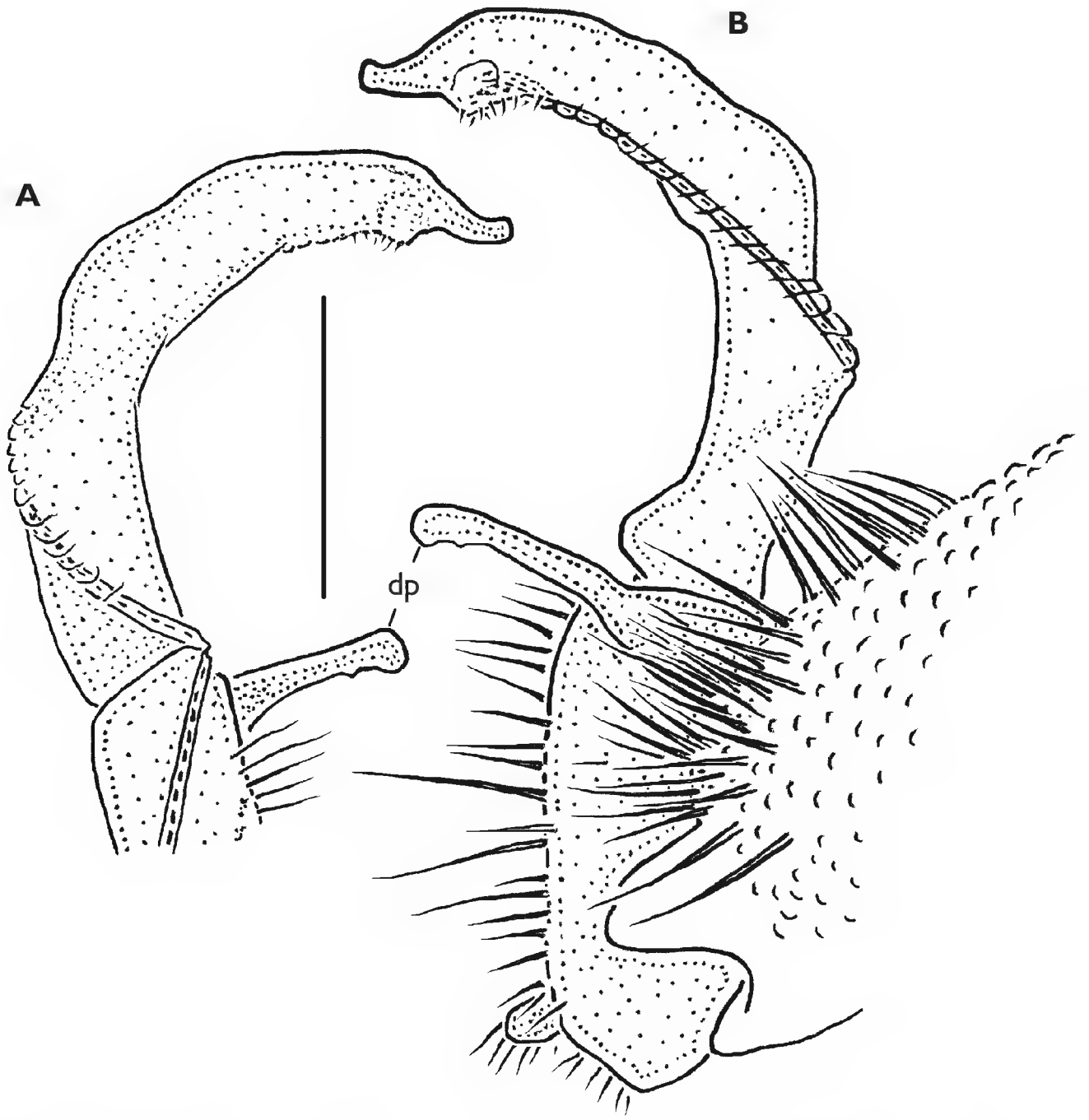


Figure 11. *Eutrichodesmus aster* sp. n., ♂ paratype from Tham Han Cave; **A, B**, left gonopod, mesal and lateral views, respectively. – Scale bar: 0.2 mm.

Description: Length of adults of both sexes ca 12-14 mm, width 2.1-2.3 mm, body broadest at segment 3 or 4. Holotype ca 12 mm long and 2.2 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 8).

Adults with 20 segments (Figs 8, 9A); body discoid, strongly flattened laterally; pattern of conglobation typical of "doratodesmids". Head, antennae (Fig. 10D), tegument (Fig. 10G), sterna (Fig. 10E), gonopod aperture and many other characters much as in *E. distinctus* sp. n.; collum rather irregularly tuberculate and only very slightly flattened medially at anterior edge (Fig. 9F). Metaterga behind collum with three transverse, rather irregular and mixostictic rows of rounded, flat, only slightly differentiated tubercles (Figs 9A-D), each crowned with a short, 2-segmented, flattened seta (Fig. 9E). Metaterga 4-19 each with a very high, slightly bifid, mid-dorsal process (Figs 8, 9A-D, 10A-C). Paraterga directed ventrolaterad up to subvertical, rather broad, surpassing level of venter (Fig. 10F); paraterga 2 strongly enlarged, very indistinctly lobulate anterolaterally (Fig. 9B). Following paraterga broadly rounded, evidently 4-lobate laterally and bilobate caudolaterally (Figs 9A-D, 10E). Limbus strongly denticulate, almost hidden by nearby abundant microvilli (Fig. 10G). Pore formula normal, ozopores poorly visible, located dorsally near base of ventrocaudal lobulation (Figs 10A, B). Epiproct short, with differentiated tubercles (Fig. 10C).

Legs relatively long, slightly surpassing edge of paraterga (Figs 10E, F).

Gonopods (Fig. 11) relatively simple. Coxae abundantly micropapillate and setose, with one normal, apicolateral lobe. Telopodite elongate, slender, slightly arcuate, with a short, bare, distofemoral process (dp) at about proximal one-third; seminal groove and acropodite (= solenomere) long, hairpad subapical.

Remarks: This pallid species shows peculiarly high mid-dorsal projections, coupled with short, distally flattened tergal setae. It is also a typical "doratodesmid", possibly another troglobite.

***Eutrichodesmus filisetiger* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:CC34CE29-FD03-4796-B19E-8EFD94686705
Figs 12-15

Type material: Vietnam, Thanh Hoa Prov., Thanh Son: Lang Kho Muong, Hang Doi Cave, hand collected, 13.XII.2003, leg. L. Deharveng and team (Vn0312-27), holotype ♂ (MNHN JC 320), paratypes: 1 ♂, 2 subad. (MNHN JC 320), 1 ♂ (SEM). Vietnam, Thanh Hoa Prov., Lang Hang: Hang Bo Muoi Cave, hand collected, 14.XII.2003, leg. L. Deharveng and team (Vn0312-33), paratype ♀ (ZMUM).

Name: To emphasize the peculiar, filiform but rather short tergal setae.

Diagnosis: Differs from congeners by the perfect volvation, coupled with the filiform tergal setae, evident metatergal lobulations, a regular pattern of tergal tuberculation and a few minor details of gonopod structure (in particular, the shape of the telopodite and a rudimentary distofemoral process).

Figure 12. *Eutrichodesmus filisetiger* sp. n., ♂ paratype from Hang Doi Cave; habitus, lateral view. (Photographed not to scale by L. Deharveng).

Description: Length of adults of both sexes ca 12-13 mm, width 2.5–2.6 mm, body broadest at segment 3 or 4. Holotype ca 12 mm long and 2.5 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 12).

Adults with 20 segments (Figs 12, 13A), pattern of conglobation typical of "doratodesmids". Head, antennae (Fig. 14A), tegument (Figs 14E, F), sterna (Fig. 14C), gonopod aperture (Fig. 14G) and many other characters (Figs 14C, D) much as in *E. distinctus* sp. n.; collum rather irregularly tuberculate and slightly flattened medially at anterior edge (Figs 13E, 14B). Metaterga behind collum with three transverse, rather regular, mixostictic rows of rounded, flat, undifferentiated tubercles (Figs 13A-F), each crowned with a short, 2-segmented, filiform seta (often broken off) (Figs 14E, F). Only last two metaterga a little elevated compared to preceding ones (Figs 12, 13A, D). Paraterga directed ventrolaterad, nearly continuing general outline of convex dorsum, rather broad, slightly surpassing level of venter, most of them evidently lobulate (Figs 13A-F, 14C); paraterga 2 strongly enlarged, evidently lobulate only anterolaterally but

not laterally (Fig. 13B). Following paraterga broadly rounded, evidently 4-lobate laterally and 3-lobate caudolaterally (Figs 13A-D, 14G). Limbus very distinctly spiculate, almost hidden by nearby abundant microvilli (Fig. 14E). Pore formula normal, ozopores very poorly visible, located dorsally near base of ventrocaudal lobulation (Figs 13C, D). Epiproct short, with regular tuberculations (Fig. 13D).

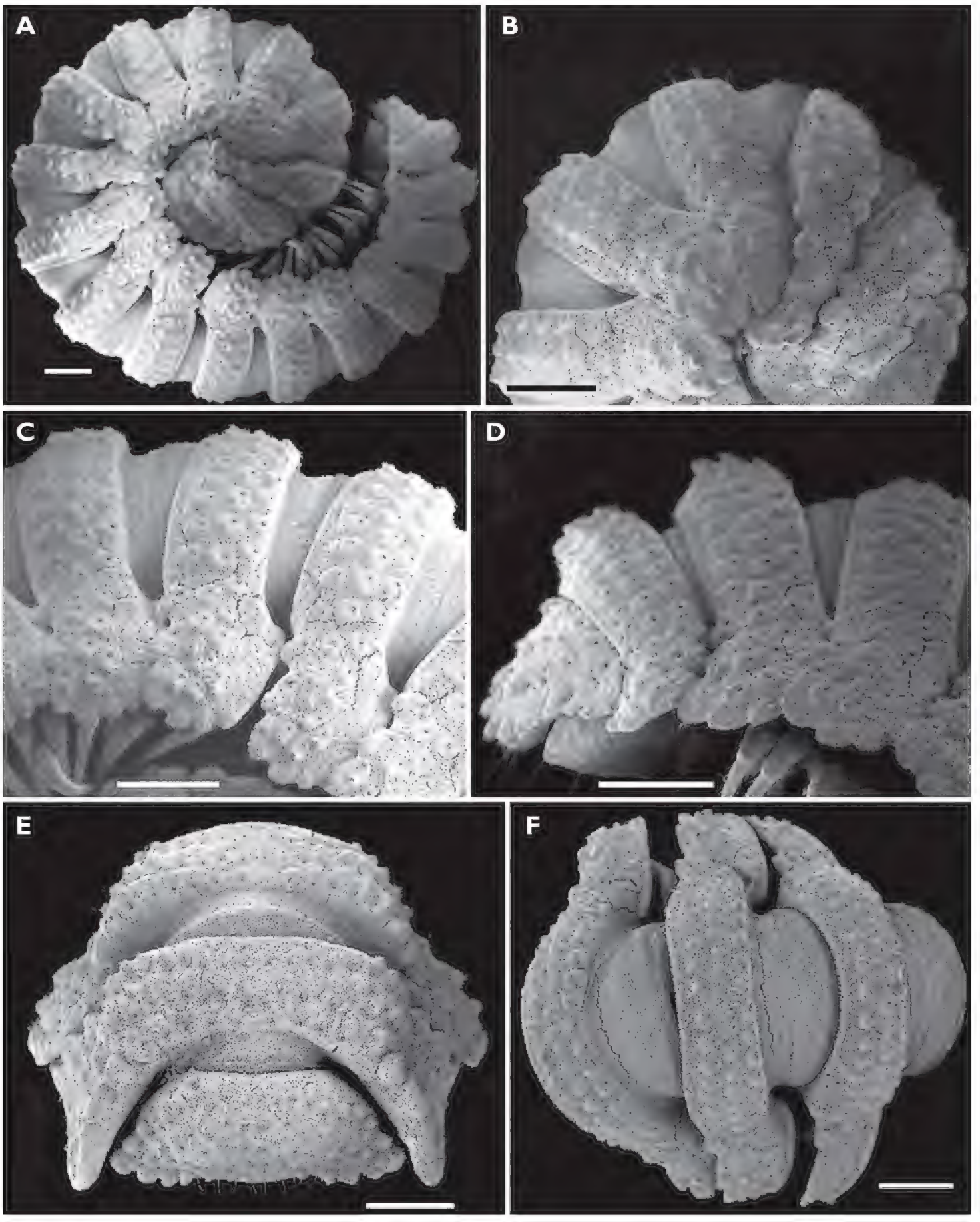


Figure 13. *Eutrichodesmus filisetiger* sp. n., ♂ paratype from Hang Doi Cave; **A**, habitus, lateral view; **B, E**, anterior part of body, lateral and frontodorsal views, respectively; **C, F**, midbody segments, lateral and dorsal views, respectively; **D**, posterior part of body, lateral view. – Scale bars: A-F, 0.5 mm.

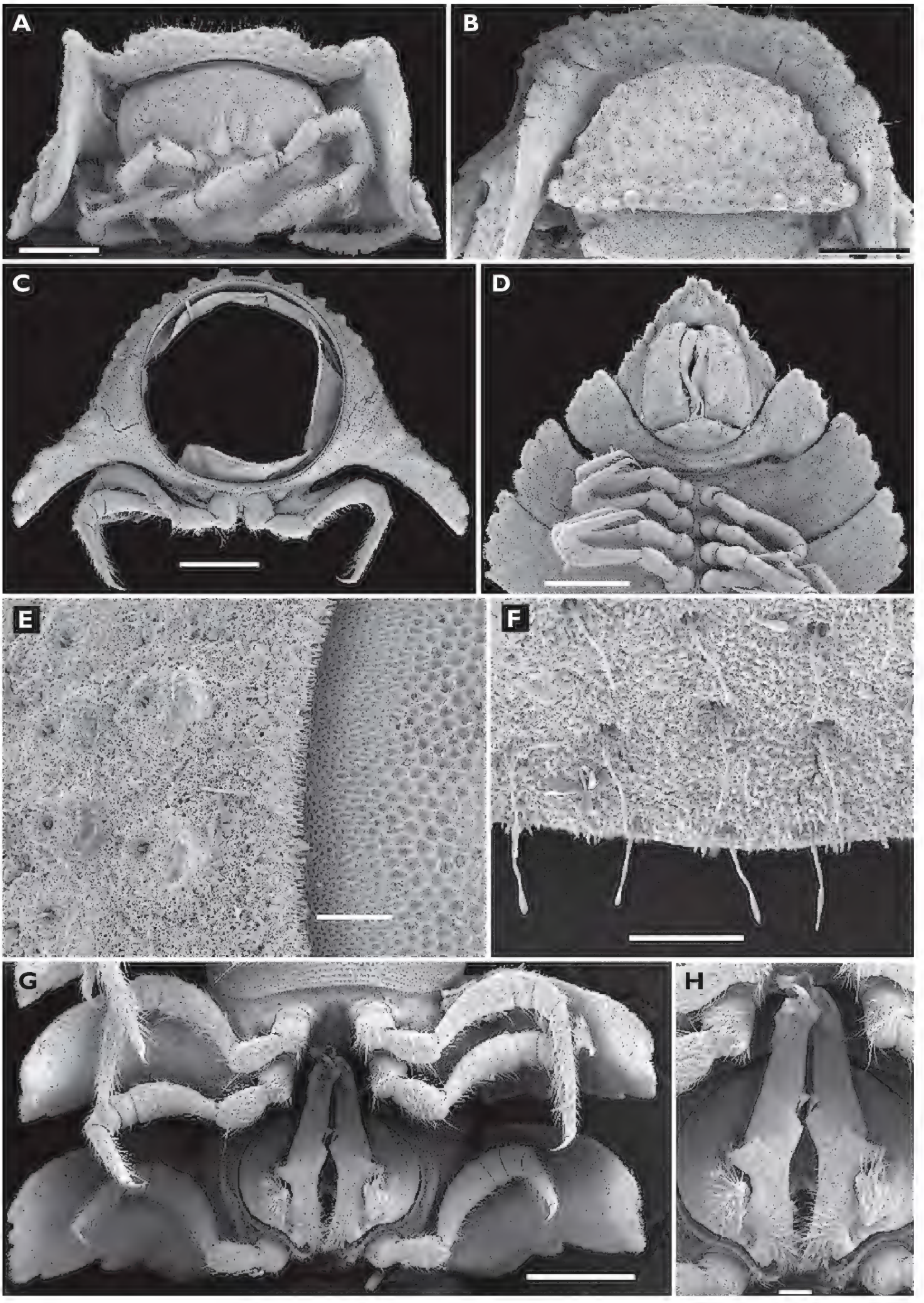
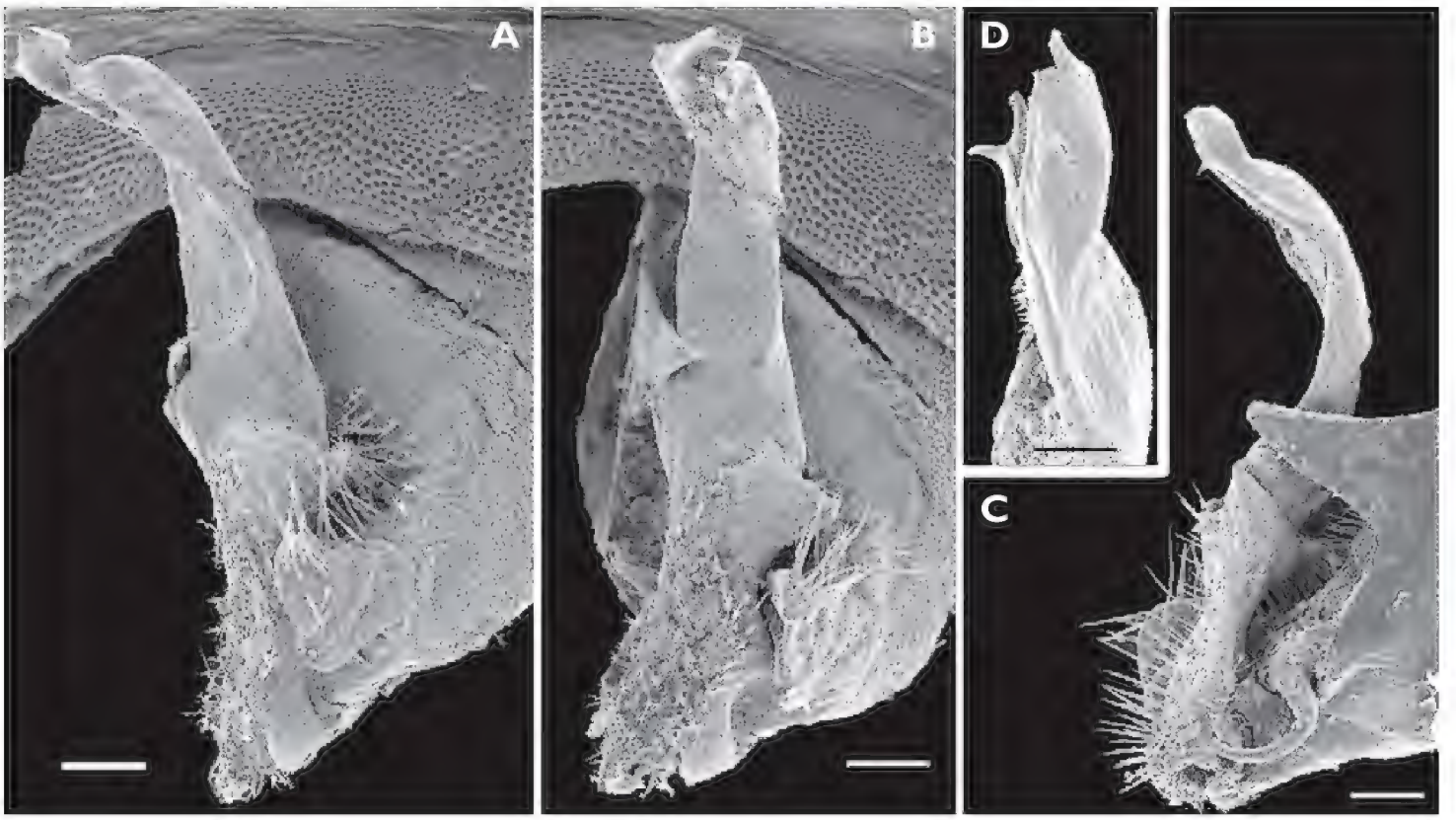


Figure 14. *Eutrichodesmus filisetiger* sp. n., ♂ paratype from Hang Doi Cave; **A**, head, dorsal view; **B**, collum, frontodorsal view; **C**, cross-section of a midbody segment, caudal view; **D**, posterior part of body, ventral view; **E**, texture of tegument, dorsal view; **F**, setae on collum; **G**, segments 6 and 7, ventral view; **H**, gonopods *in situ*. – Scale bars: A-D, G, 0.5 mm; E, F, H, 0.1 mm.



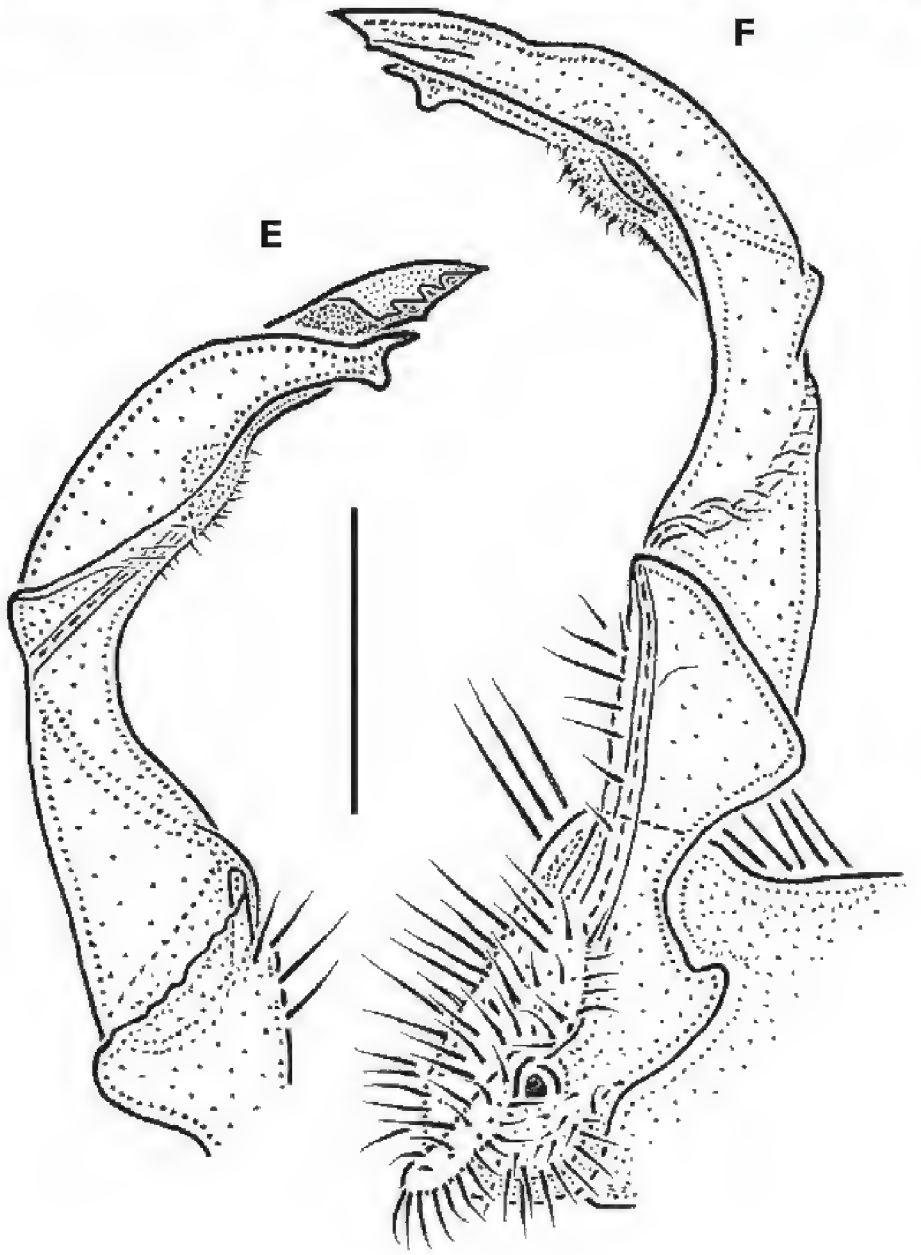


Figure 15. *Eutrichodesmus filisetiger* sp. n., ♂ paratypes from Hang Doi Cave; **A-F**, gonopod, subventral, ventral, sublateral, mesal, lateral and mesal views, respectively. – Scale bars: A-C, 0.01 mm; D, 0.05 mm; E, F, 0.2 mm.

Legs relatively long and slender, slightly reaching edge of paraterga (Figs 14C, G).

Gonopods (Figs 14G, H, 15A-F) relatively complex. Coxae abundantly micropapillate and setose, with two conspicuous lobes: one normal, apicolateral, the other unusual, subtriangular, median, both apparently to control telopodite movements. Telopodite elongate, slender, slightly arcuate, with only a rudimentary distofemoral process at about midway (barely seen in lateral view as a short prong in a kind of pocket) and an evident hairpad at distal one-third of acropodite (= solenomere), also marking a branching point of two long, slender, apical pieces, one lateral, bifid, a little shorter and well-sclerotized, the other lamellar, pointed and dentate.

Remarks: This rather large, pallid species shows filiform tergal setae and only poorly differentiated metatergal tubercles. It is also a typical "doratodesmid", possibly still another troglobite.

***Eutrichodesmus curticornis* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:AEBAEF74-7FF7-4E99-8108-D0D85ACE06C3
Figs 16-18

Type material: Vietnam, Nghê An Prov., Anh Son: Hoi Son, Hang Lung Bo Cave, hand collected, 19.I.2003, leg. L. Deharveng and A. Bedos (VIET-901), holotype ♂ (MNHN JC 321), paratypes: 1 ♀ (MNHN JC 321), 1 ♀ (SEM).

Figure 16. *Eutrichodesmus curticornis* sp. n., ♀ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

Name: To emphasize the unusually short antennae.

Diagnosis: Differs from congeners by the perfect volvation, coupled with the very short antennae, legs and paraterga, the contiguous paramedian tubercles above the antennal sockets, the regular mixostictic pattern of metatergal tuberculation and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Description: Length of adults of both sexes ca 4.7-5.3 mm, width 0.65–0.7 mm, body broadest at segment 3 or 4. Holotype ca 4.7 mm long and 0.65 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 16).

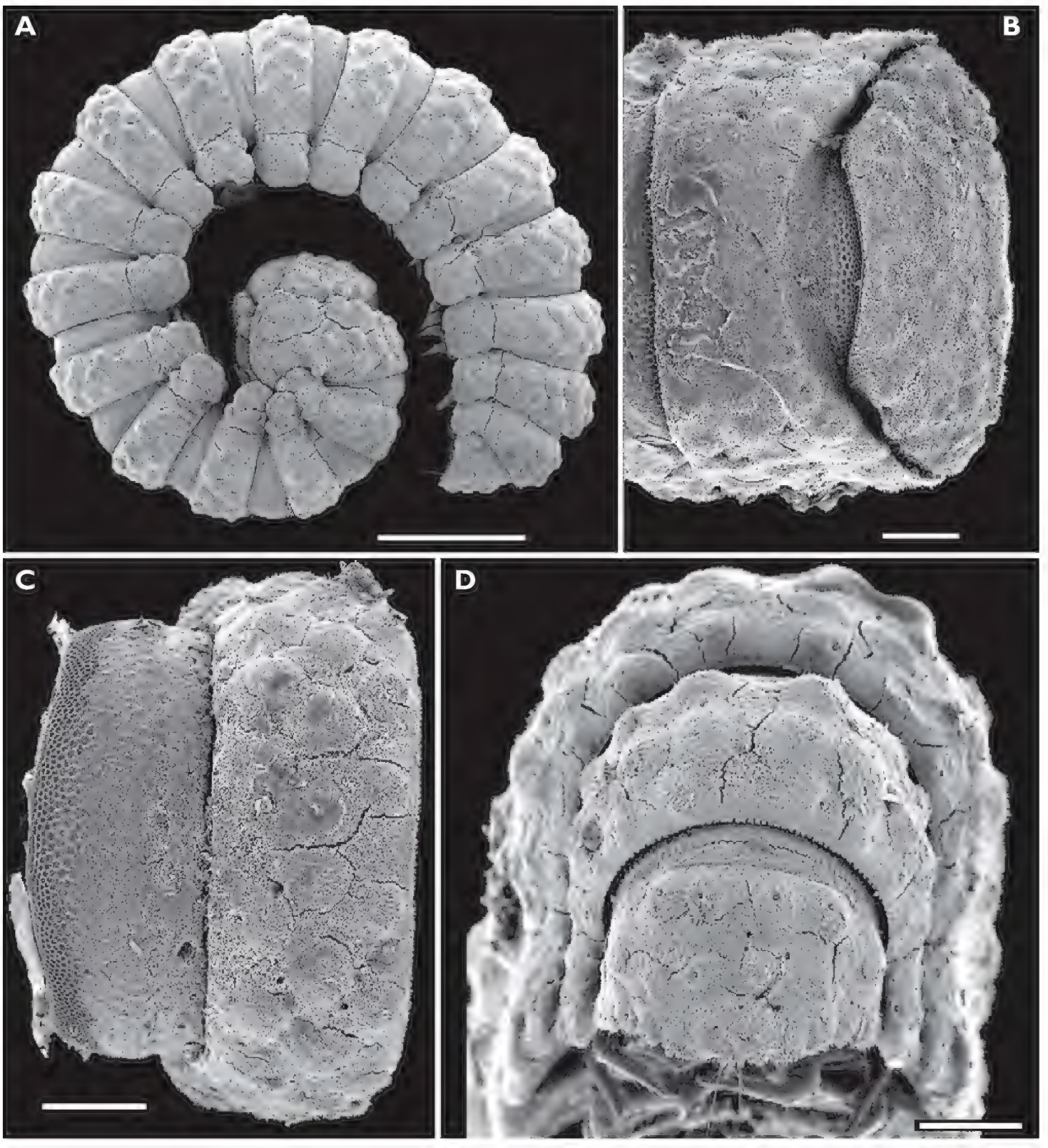


Figure 17. *Eutrichodesmus curticornis* sp. n., ♀ paratype; **A**, habitus, lateral view; **B**, anterior part of body, dorsal view; **C**, midbody segment, dorsal view; **D**, posterior part of body, caudal view. Scale bars: A, 1.0 mm; B-D, 0.1 mm.

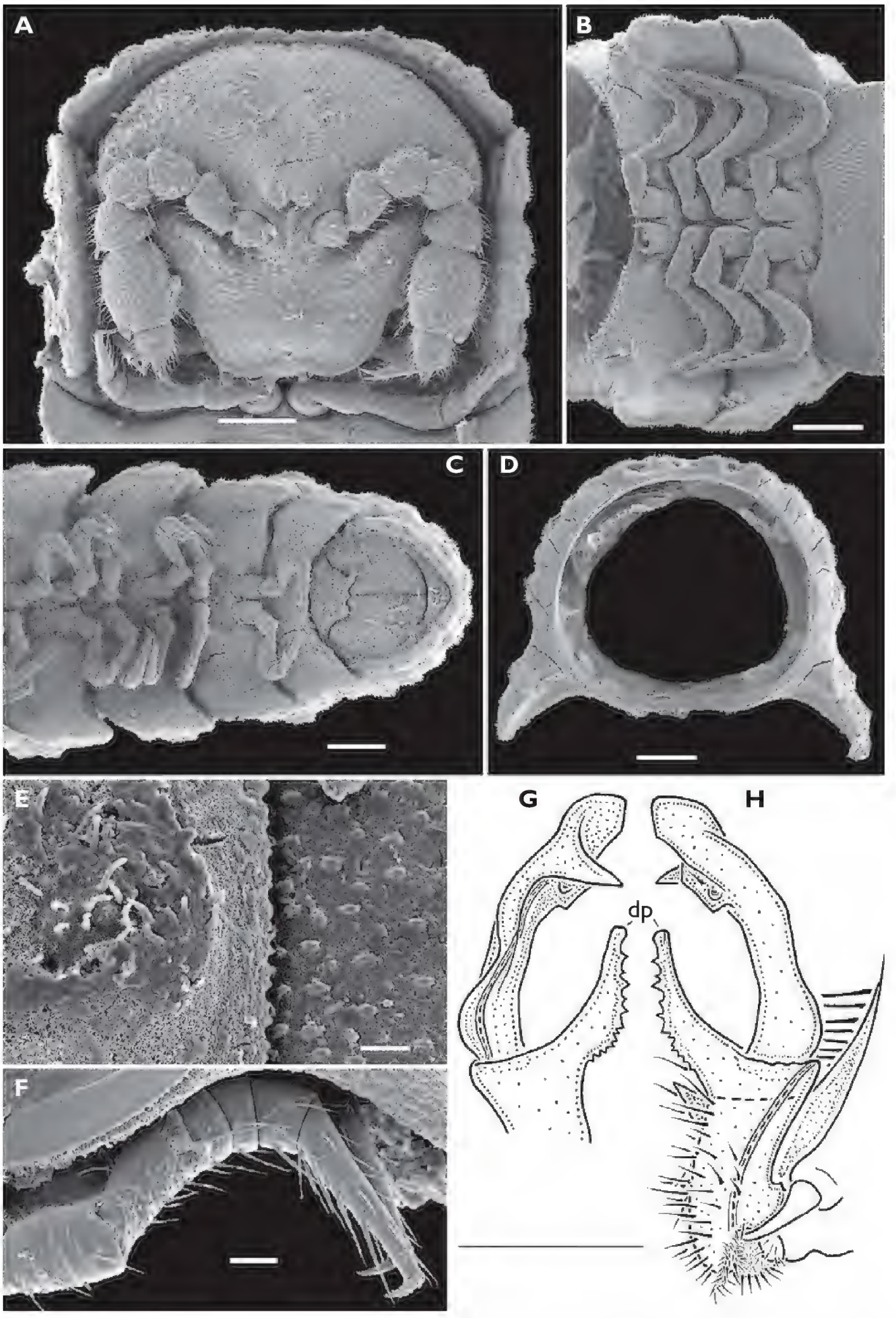


Figure 18. *Eutrichodesmus curticornis* sp. n., ♀ paratype (A-F) and ♂ holotype (G-H); **A**, anterior part of body, ventral view; **B**, midbody segments, ventral view; **C**, posterior part of body, ventral view; **D**, cross-section of a midbody segment, caudal view; **E**, texture of tegument; **F**, legs, caudal view; **G, H**, right gonopod, lateral and mesal views, respectively. – Scale bars: A-D, G, 0.1 mm; E, 0.01 mm; F, H, 0.02 mm.

Adults with 20 segments (Figs 16, 17A), pattern of conglobation typical of "doratodesmids". Head (Fig. 18A) with a contiguous pair of paramedian tubercles above antennal sockets; antennae very short and clavate, but tegument (Fig. 18E) and many other characters (Figs 18B, C, F) much as in *E. distinctus* sp. n.; collum rather regularly tuberculate (Fig. 17B). Metaterga behind collum with three transverse, regular, mixostictic rows of rounded, flat, undifferentiated tubercles (Figs 17A, C), each crowned with a broken-off seta (Fig. 18E). Paraterga subvertical, rather wide, slightly surpassing level of venter, with only a slight impression at base and nearly continuing general outline of convex dorsum (Fig. 18D); paraterga 2 (Figs 17A, 18A) evidently lobulate only anterolaterally but not laterally (Fig. 17A). Following paraterga broadly rounded, very slightly bilobate laterally and unilobate caudolaterally (Figs 17A, 18B). Limbus rather irregularly crenulate, almost hidden by nearby abundant microvilli (Fig. 18E). Pore formula normal, ozopores poorly visible, located dorsally near base of ventrocaudal lobulation (Fig. 17A). Epiproct short, with only slightly differentiated tubercles (Fig. 17D).

Legs very short and stout, barely reaching edge of paraterga (Fig. 18F).

Gonopods (Figs 18G, H) relatively complex. Coxae abundantly micropapillate and setose, with a usual, apicolateral lobe. Telopodite elongate, slender, only very slightly arcuate, with a marked, denticulate distofemoral process (dp) at about midway and an evident distolateral tooth; seminal groove terminating without hairpad at base of the tooth.

Remarks: This pallid species shows short antennae, legs and paraterga, all these traits apparently being related to the small body size. It is also a typical "doratodesmid", possibly yet one more troglobite.

***Eutrichodesmus asteroides* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:C1DBB0D8-E640-42A8-9307-7E0CFB894BC5
Figs 19-22

Type material: Vietnam, Quang Binh Prov., Cha Noi: Hang Cha Noi Cave, hand collected, 8.I.1995, leg. L. Deharveng and A. Bedos (VIET-064), holotype ♂ (MNHN JC 322), paratypes: 1 ♂ (MNHN JC 322), 1 ♀ (SEM). Vietnam, Quang Binh Prov., Dong Hoi: Grotte de Troc, hand collected, 15.III.1997, leg. A. Bedos and Long (VIET-407), paratypes: 3 ♂, 2 ♀, 2 juv. (MNHN JC 322), 1 ♂ (ZMUM).

Name: To emphasize the nearly star-shaped but broad body of the volvated animal.

Diagnosis: Differs from congeners by the peculiar, subtriangular, rather high, mid-dorsal crests on metaterga 4-18, coupled with 19 body segments, the relatively wide paraterga and a few minor details of gonopod structure (in particular, the shape of the telopodite and a rudimentary distofemoral process).

Description: Length of adults of both sexes ca 8.0-8.5 mm, width 2.1-2.5 mm, body broadest at segment 3 or 4. Holotype ca 8.0 mm long and 1.9 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 19).

Figure 19. *Eutrichodesmus asteroides* sp. n., ♂ paratype from Hang Cha Noi Cave; habitus, lateral view. (Photographed by L. Deharveng).

Adults with 19 segments (Figs 19, 20A); body subasteriform but relatively broad, non-discoid; volvation complete even though paraterga relatively wide. Head (Fig. 21C) with a very distinctly separated pair of paramedian tubercles above antennal sockets; antennae relatively long and slender; tegument (Figs 22A, C) and many other characters (Figs 21D, E, 22A-D) much as in *E. distinctus* sp. n.; collum very faintly tuberculate, almost smooth (Fig. 20E). Metaterga behind collum with three transverse, rather regular, mixostictic rows of rounded, flat, well-differentiated tubercles, mid-dorsal ones in anterior and middle rows being especially high and fused into a high double club of subtriangular shape in lateral view (Figs 20A-F, 21A, B); tergal setation missing (Figs 22A-C). Paraterga directed ventrolaterad, rather long and broad, well reaching level of venter (Figs 21B, D-F); paraterga 2 rather poorly lobulate only anterolaterally and caudally (Fig. 20B). Following paraterga broadly rounded, unilobate only caudolaterally. Limbus with very broad crenulations (Figs 22B). Pore formula normal, ozopores poorly visible, located dorsomedially of lateral margin of paraterga (Fig. 22A).

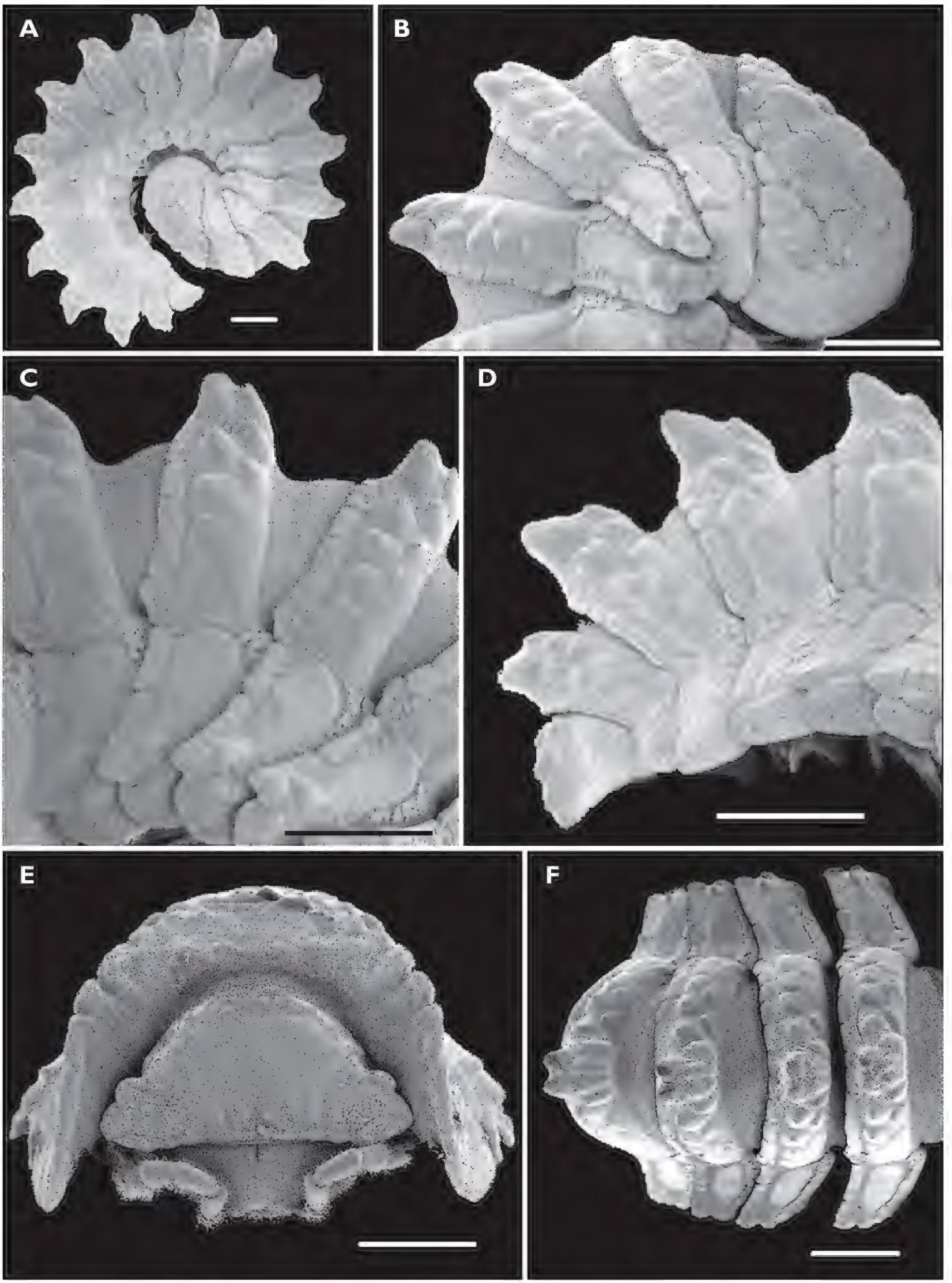


Figure 20. *Eutrichodesmus asteroides* sp. n., ♀ paratype from Hang Cha Noi Cave; **A**, habitus, lateral view; **B**, **E**, anterior part of body, lateral and frontal views, respectively; **C, F**, midbody segments, lateral and dorsal views, respectively; **D**, posterior part of body, lateral view. – Scale bars: A-F, 0.5 mm.

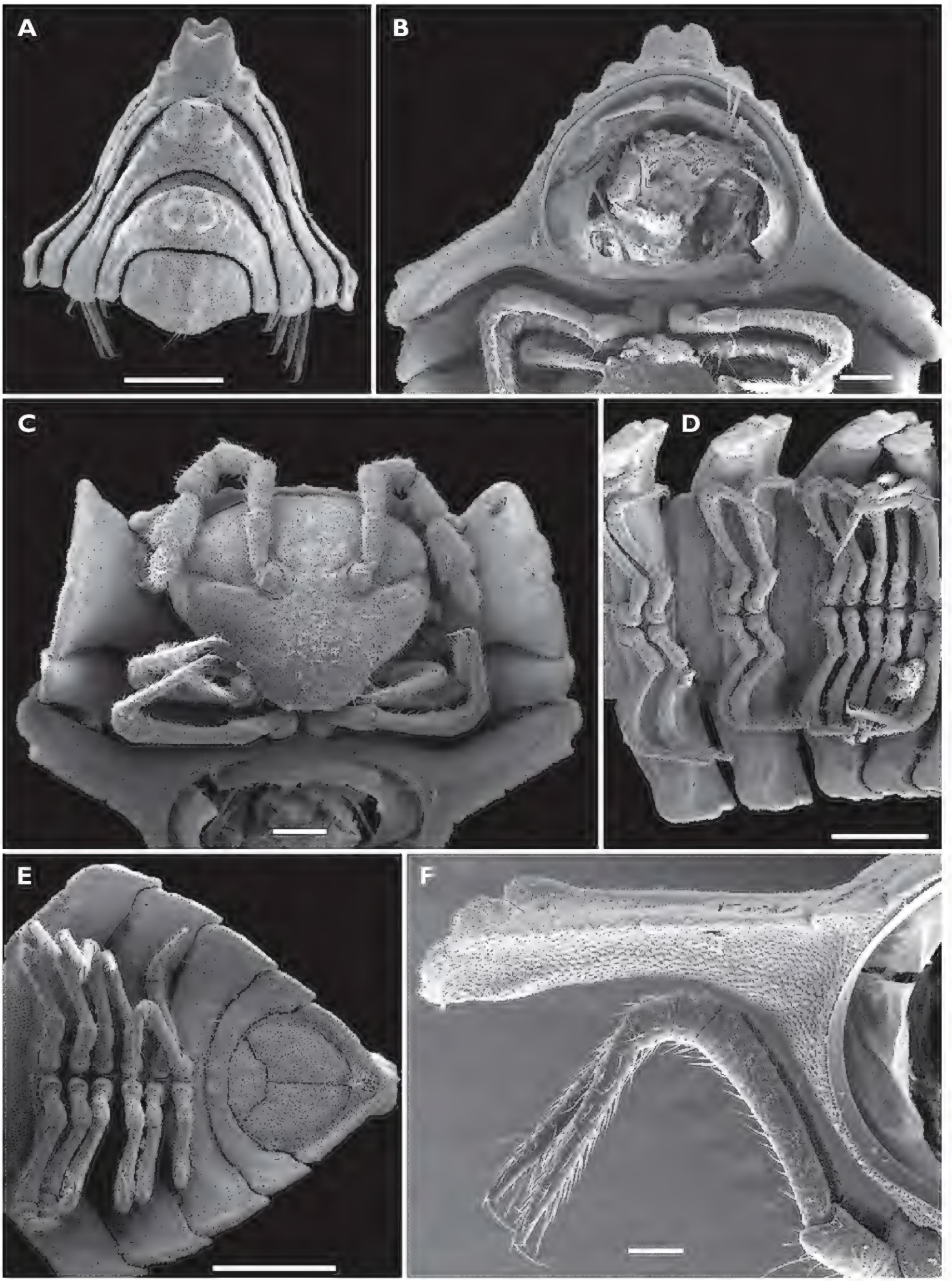
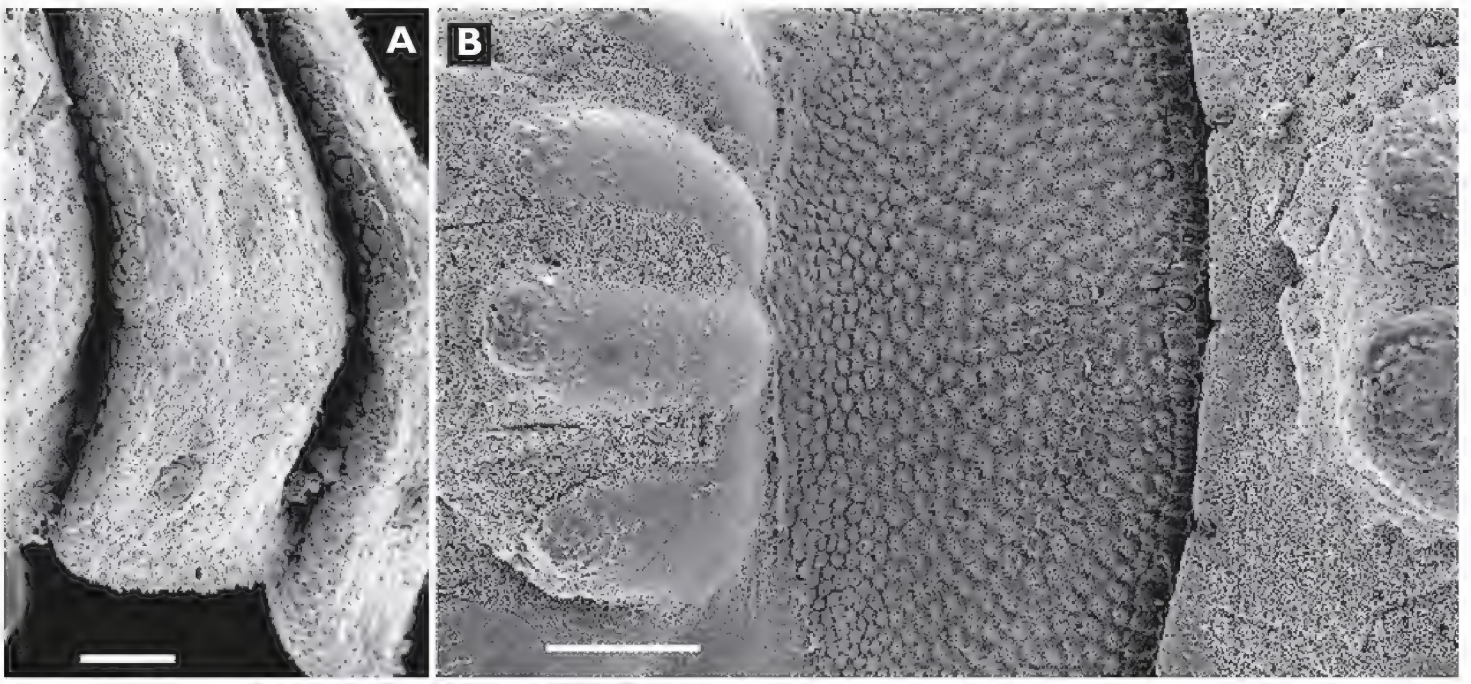
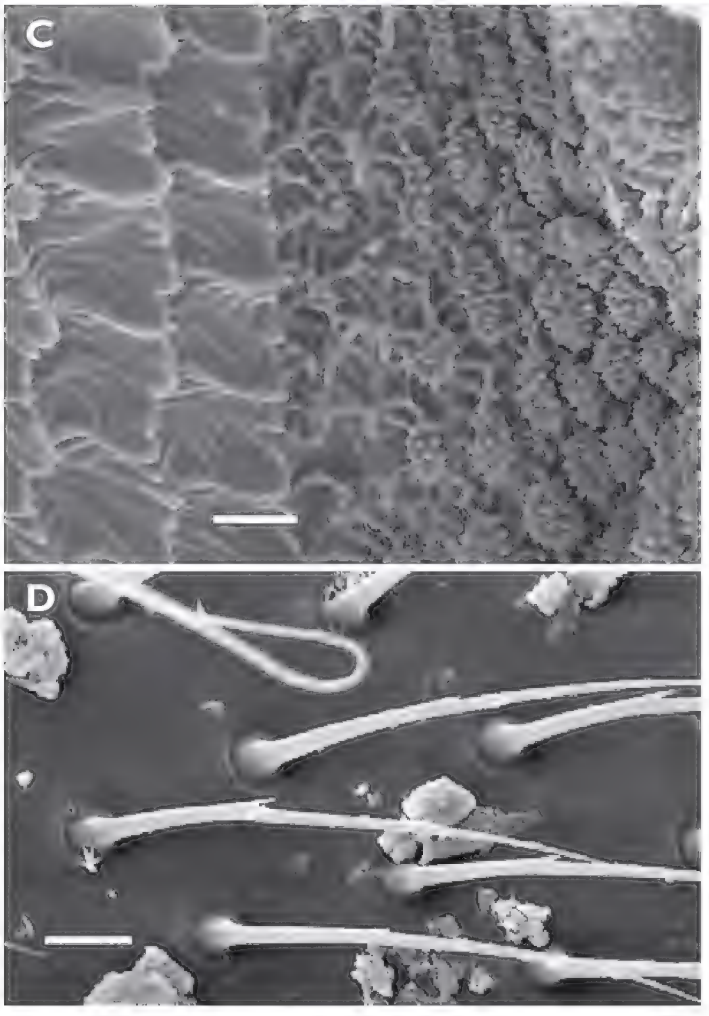


Figure 21. *Eutrichodesmus asteroides* sp. n., ♀ paratype from Hang Cha Noi Cave; **A, E**, posterior part of body, caudal and ventral views, respectively; **B**, cross-section of a midbody segment, caudal view; **C**, anterior part of body, ventral view; **D**, midbody segments, ventral view; **F**, midbody paratergum and legs, caudal view. – Scale bars: A, D, E, 0.5 mm; B, C, 0.2 mm; F, 0.1 mm.

Legs relatively long and slender, reaching edge of paraterga (Figs 21B, D-F).

Gonopods (Figs 22E, F) relatively simple. Coxae abundantly micropapillate but only with two macrosetae near base a small apicolateral lobe. Telopodite elongate, slender, evidently arcuate, with a rudimentary, prong-shaped distofemoral process (dp) at about midway, an evident, mesal, rounded lobe at about midway of acropodite (= solenomere), and a bipartite apical part starting at a hairless pad terminating seminal





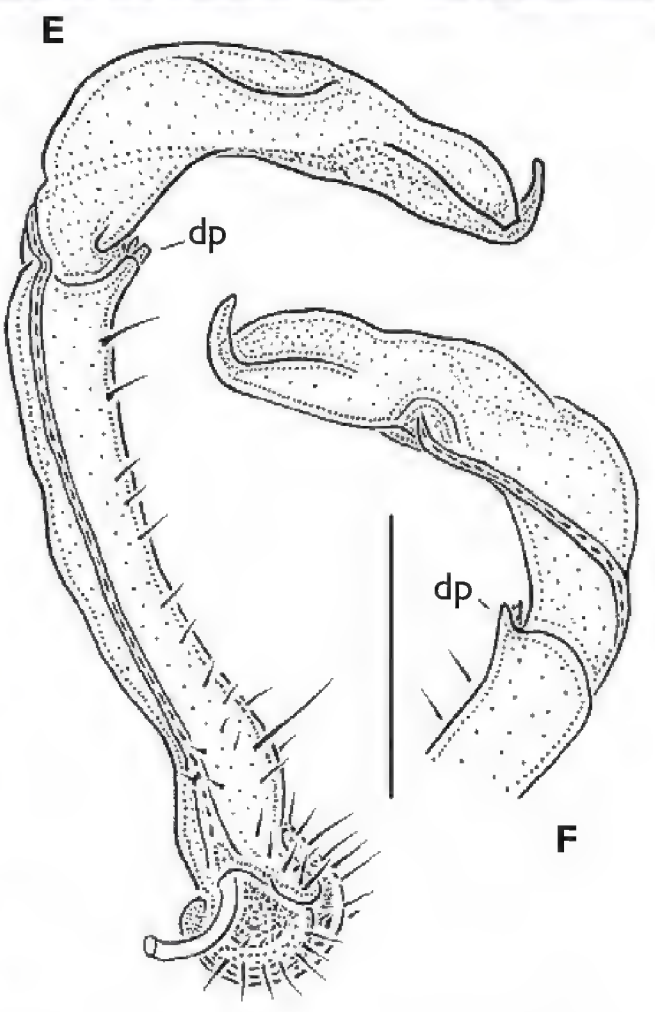


Figure 22. *Eutrichodesmus asteroides* sp. n., ♀ (A-D) and ♂ (E-F) paratypes from Hang Cha Noi Cave; **A**, midbody metaterga, sublateral view; **B, C**, texture of tegument, dorsal view; **D**, setae on antennae; **E, F**, left gonopod, mesal and lateral views, respectively. – Scale bars: A, 0.05 mm; B, 0.1 mm; C, 0.01; D, 0.005 mm; E, F, 0.2 mm.

groove; mesal of apical branches shorter and digitiform, whereas lateral one a little longer and unciform.

Remarks: Because this species has only been taken from caves, it can possibly be considered as a troglobite.

***Eutrichodesmus griseus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:E7EB907C-AA5B-4612-B292-403142A55D5B
Figs 23-26

Type material: Vietnam, Kien Giang Prov., Kien Luong: Hon Chong, Nui Hon Chong, outside Cave 2 near Hang Hai Côt, grasses, soil, Berlese extraction, 27.I.2003, leg. L. Deharveng and A. Bedos (VIET-923), holotype ♂ (MNHN JC 323), paratypes: 1 ♂, 1 ♀ (MNHN JC 323), 1 ♀ (SEM).

Name: To emphasize the greyish coloration of the vertex, collum, metaterga and most of the telson.

Diagnosis: Differs from congeners by the peculiar, grey to blackish coloration, coupled with the relatively short and high paraterga (thus the body apparently not capable of complete volvation) and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Figure 23. *Eutrichodesmus griseus* sp. n., ♀ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

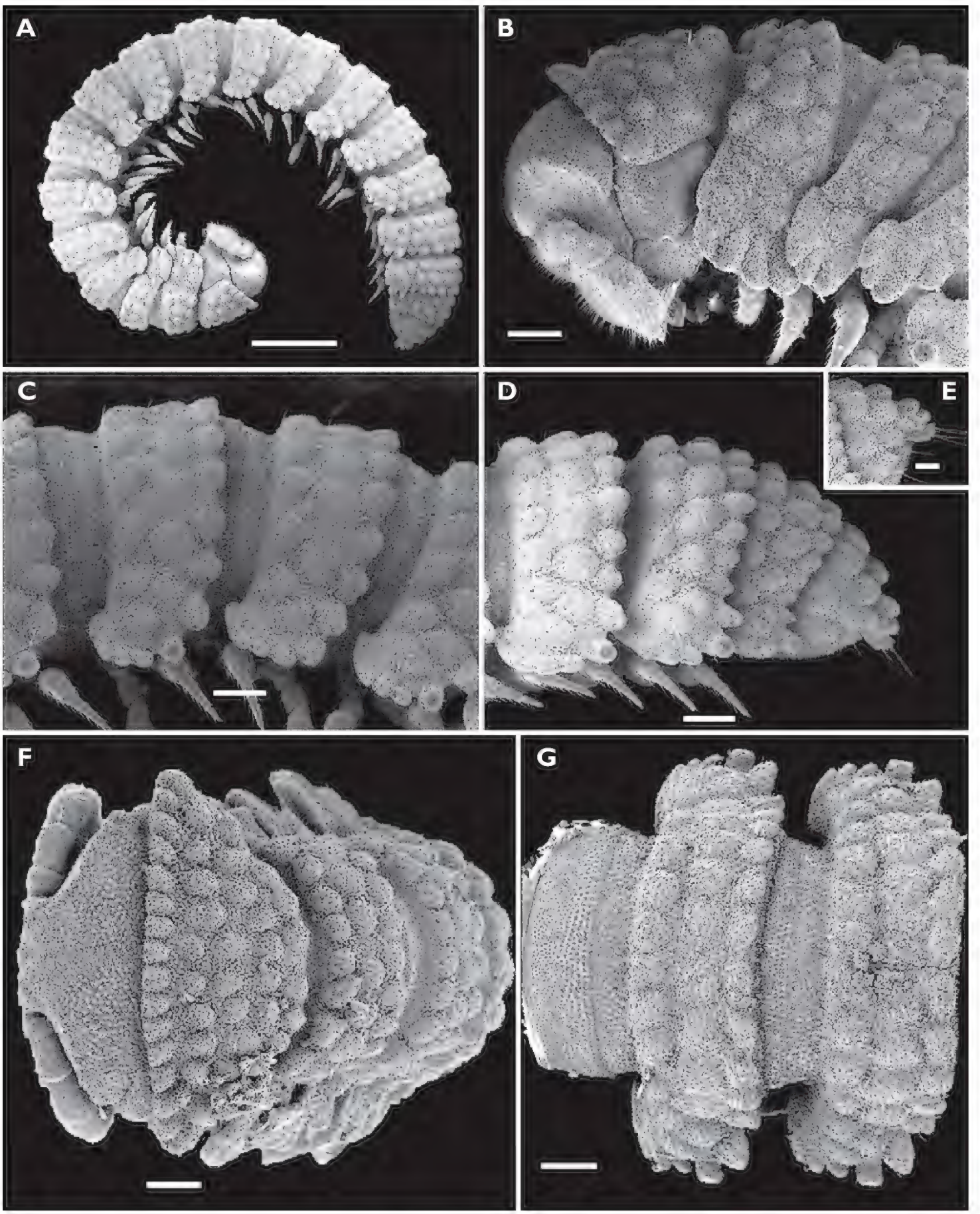


Figure 24. *Eutrichodesmus griseus* sp. n., ♀ paratype; **A**, habitus, lateral view; **B**, **F**, anterior part of body, lateral and frontal views, respectively; **C, G**, midbody segments, lateral and dorsal views, respectively; **D**, posterior part of body, lateral view; **E**, epiproct, dorsolateral view. – Scale bars: A, 0.5 mm; B-G, 0.1 mm.

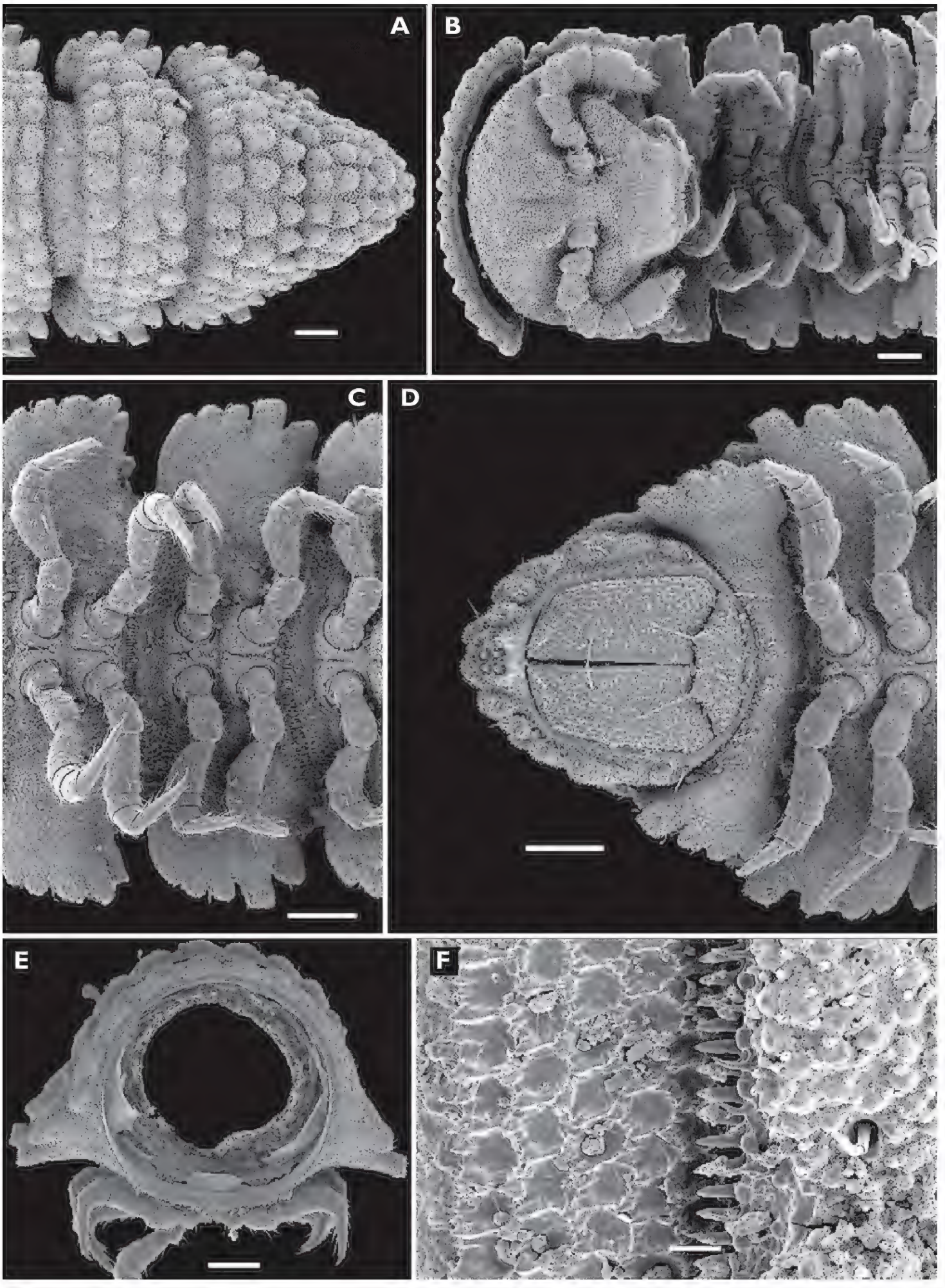


Figure 25. *Eutrichodesmus griseus* sp. n., ♀ paratype; **A**, **D**, posterior part of body, dorsal and ventral views, respectively; **B**, anterior part of body, ventral view; **C**, midbody segments, ventral view; **E**, cross-section of a midbody segment, caudal view; **F**, texture of tegument, dorsal view. – Scale bars: A-E, 0.1 mm; F, 0.01 mm.

Description: Length of adults of both sexes ca 6.0-6.5 mm, width 0.7–0.75 mm, body broadest at segment 3 or 4. Holotype ca 4.5 mm long and 2.5 mm wide. Coloration of vertex, collum, following metaterga, and of dorsal and lateral parts of telson greyish to dark grey. Clypeolabral part of head, venter and legs contrastingly pallid (Fig. 23). Holotype light grey.

Adults with 20 segments (Figs 23, 24A), volvation apparently incomplete due to relatively short paraterga. Head (Fig. 25B) with a poorly separated pair of paramedian tubercles above antennal sockets; antennae relatively short and clavate; tegument (Fig. 25F) and many other characters (Figs 25C-E) much as in *E. distinctus* sp. n.; collum

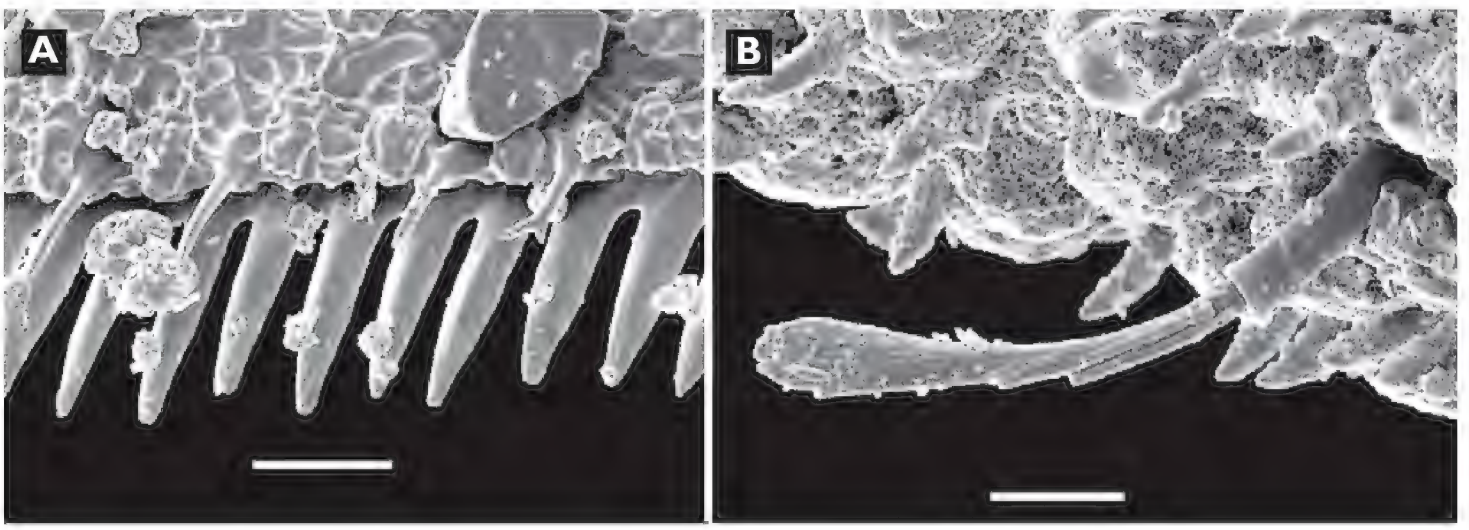


Figure 26. *Eutrichodesmus griseus* sp. n., paratypes ♀ (A, B) and ♂ (C, D, E); **A**, limbus, dorsal view; **B**, metatergal seta, sublateral view; **C-E**, left gonopod, mesal, lateral and subfrontal views, respectively. – Scale bars: A, 0.01 mm; B, 0.005 mm; C-E, 0.2 mm.

rather regularly tuberculate, anterior row of tubercles especially dense and directed dorsofrontally, thus slightly resembling a pyrgodesmid condition (Figs 24A, B, F). Metaterga behind collum with three transverse, regular, nearly isostictic rows of rounded, flat, undifferentiated tubercles (Figs 24A-G), each crowned with a short, 2-segmented, conspicuously denticulate and slightly claviform seta (Fig. 26B). Paraterga directed ventrolaterad, short but rather broad, barely reaching level of venter, nearly continuing general outline of convex dorsum (Figs 24A-D, 25E); paraterga 2 (Fig. 24B) evidently lobulate only laterally. Following paraterga broadly rounded, evidently 3- to 5-lobate laterally, at least bilobate also caudolaterally (Figs 24A-D, G). Limbus distinctly spinulate (Fig. 26A), almost hidden by nearby abundant microvilli (Fig. 25F). Pore formula normal, ozopores located on top of porosteles (always caudalmost lateral lobulation) (Figs 24A-D, G). Epiproct rather heavily tuberculate (Figs 24D, E).

Legs relatively short and stout, barely reaching edge of paraterga (Figs 25C-E).

Gonopods (Figs 26C-E) relatively simple. Coxae abundantly micropapillate but only with two macrosetae near base of a small apicolateral lobe. Telopodite elongate, rather slender, evidently arcuate, with a rudimentary, subtriangular, distofemoral process (dp) at about midway and an evident lateral, digitiform solenomere bearing a large hairpad apically and subapically, and a simple dentiform acropodite mesally.

Remarks: Because this pigmented species obviously shows incomplete volvation, it is not a typical "doratodesmid", definitely epigean. Moreover, because of the elevated anterior row of tubercles on the collum, superficially it slightly resembles certain Pyrgodesmidae.

***Eutrichodesmus multilobatus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:9236AEA3-5110-48E6-BD00-2ABB1CBAADC2
Figs 27-30

Type material: Laos, Luang Prabang Prov., Nong Kiaw: Tham Pha Kouang, Cave B, hand collected, 22.XII.1999, leg. L. Deharveng and A. Bedos (LAO-099), holotype ♂ (MNHN JC 324), paratypes: 1 ♂ (MNHN JC 324), 1 # M (ZMUM), 1 ♀ (SEM).

Name: To emphasize the mostly 5-lobulated paraterga.

Diagnosis: Differs from congeners by the peculiar, evidently and only laterally 5-lobulated paraterga, coupled with very distinct but only slightly differentiated metatergal tuberculation and a few minor details of gonopod structure (in particular, the shape of the telopodite and distofemoral process).

Description: Length of adults of both sexes ca 6.0-6.5 mm, width 1.1-1.2 mm, body broadest at segment 3 or 4. Holotype ca 6.0 mm long and 1.1 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 27).

Adults with 20 segments (Figs 27, 28A), volvation complete, although paraterga relatively short. Head (Fig. 28G) with a poorly separated pair of paramedian tubercles above antennal sockets; antennae relatively short and clavate (Fig. 29D); tegument (Figs 29E, F) and many other characters (Figs 28F, G, 29A, B) much as in *E. distinc-*

Figure 27. *Eutrichodesmus multilobatus* sp. n., ♀ paratype; habitus, lateral view. (Photographed not to scale by L. Deharveng).

tus sp. n.; collum and following metaterga heavily tuberculate (Figs 28A, C, D, G). Metaterga behind collum with three transverse, irregular, mixostictic rows of rounded, mostly very clear, differentiated tubercles slightly but steadily growing higher in anterior and, especially, middle rows both toward axial line and telson (Figs 27, 28A-F), and becoming particularly evident on segments 18 and 19 (Fig. 28F). Metatergal setae mostly broken off, otherwise short, filiform, helically striate as in Fig. 29F. Paraterga directed ventrolaterad, yet markedly interrupting contour of convex dorsum, rather short but broad, reaching level of venter (Figs 28F, 29C); paraterga 2 evidently lobulate only anteriorly and laterally (Figs 28A, C, G). Following paraterga narrowly rounded caudally, always subtruncated and quite evidently 5-lobate laterally, non-lobate caudolaterally (Figs 28A, B, D, 29A). Limbus distinctly crenulate, almost hidden by nearby abundant microvilli (Fig. 29E). Pore formula normal, ozopores located on top of porosteles (always penultimate lateral lobulation) (Figs 28A, B, D, E).

Legs relatively short and stout, barely reaching edge of paraterga (Figs 29A, C).

Gonopods (Fig. 30) relatively simple. Coxae abundantly micropapillate, but only with a few macrosetae. Telopodite elongate, slightly arcuate, with a large, papillate, distofemoral process (dp) at about midway and a very simple solenomere bearing a small group of minute hairs (but no pad!) subapically at base of a tiny, rounded, terminal hook.

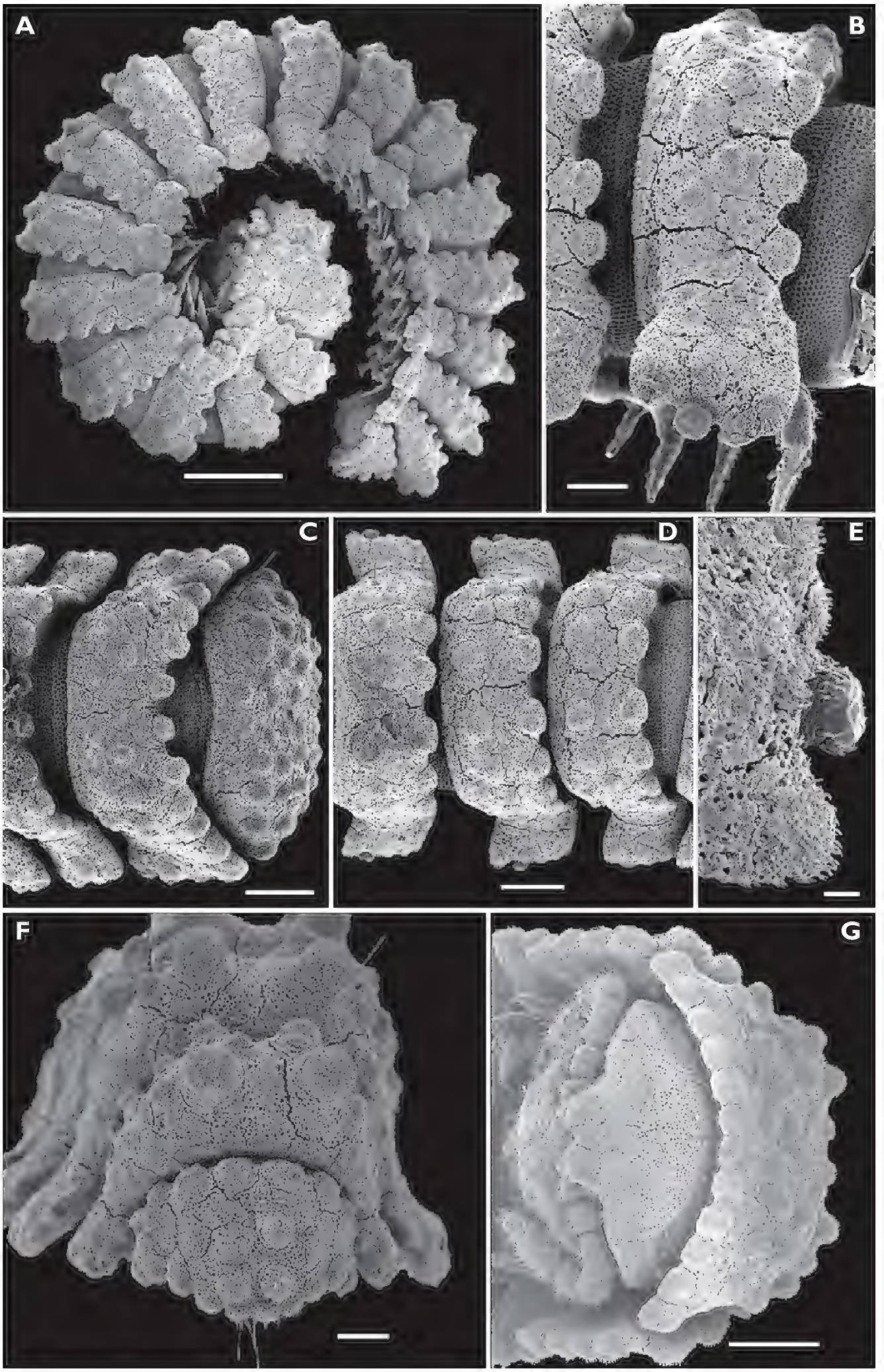


Figure 28. *Eutrichodesmus multilobatus* sp. n., ♀ paratype; **A**, habitus, lateral view; **B, D**, midbody segments, lateral and dorsal views, respectively; **C, G**, anterior part of body, dorsal and ventral views, respectively; **E**, lateral edge of paratergum with ozopore, dorsal view; **F**, posterior part of body, caudal view. – Scale bars: A, 0.5 mm; B, F, 0.1 mm; C, D, G, 0.2 mm; E, 0.02 mm.

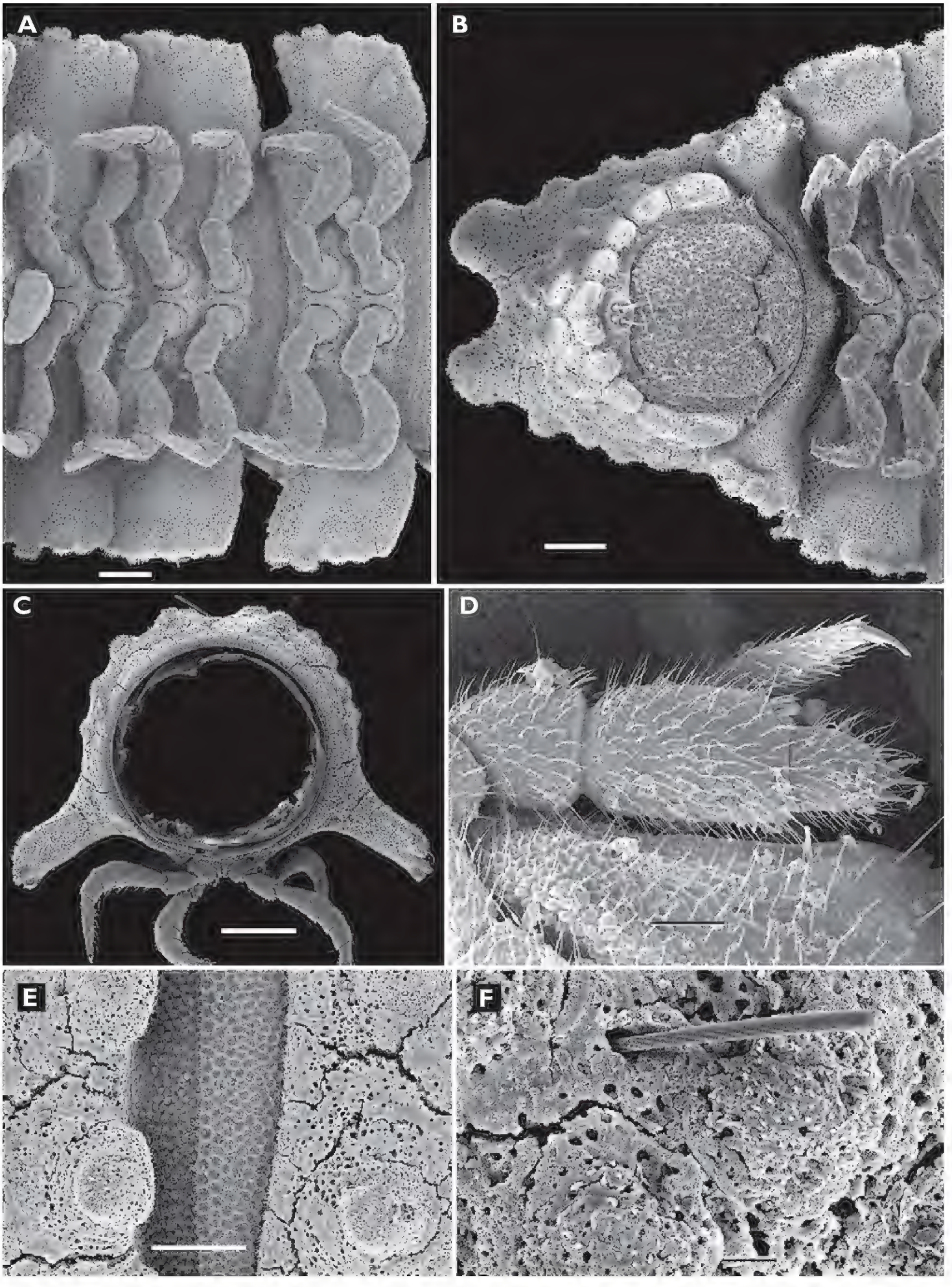


Figure 29. *Eutrichodesmus multilobatus* sp. n., ♀ paratype; **A**, midbody segments, ventral view; **B**, posterior part of body, ventral view; **C**, cross-section of a midbody segment, caudal view; **D**, part of head with left antenna, subdorsal view; **E**, texture of tegument, dorsal view; **F**, metatergal seta. – Scale bars: A, B, E, 0.1 mm; C, 0.2 mm; D, 0.05 mm; F, 0.02 mm.

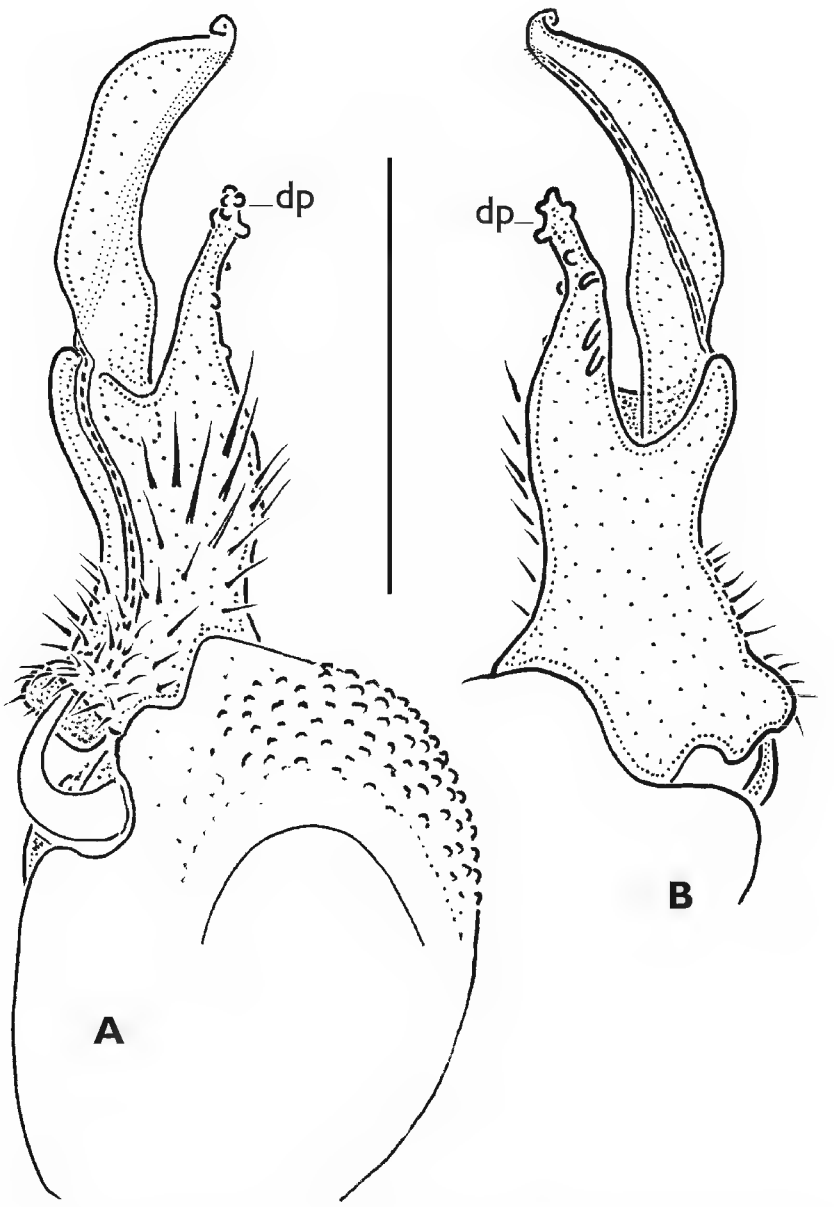


Figure 30. *Eutrichodesmus multilobatus* sp. n., ♂ paratype; **A, B**, right gonopod, mesal and lateral views, respectively. – Scale bar: 0.3 mm.

Remarks: This small-bodied, pallid species shows peculiar patterns of metatergal tuberculation and paratergal lobulation. It is a typical "doratodesmid", possibly still one more troglobite.

***Eutrichodesmus reductus* Golovatch, Geoffroy, Mauriès & VandenSpiegel, sp. n.**
urn:lsid:zoobank.org:act:1726A727-8FC2-4BF8-807D-8DFC1C54380C
Figs 31-33

Type material: Indonesia, Sulawesi Selatan, kab. Maros: Samanggi, Gua Saripa Cave, hand collected, 18.VIII.1990, leg. A. Bedos and L. Deharveng (SULS-214), holotype ♂ (MZB), paratypes: 1 ♂ (MNHN JC 325), 1 ♀ (SEM).

Name: To emphasize the strongly underdeveloped paraterga 2 and lack of metatergal tuberculation.

Diagnosis: Differs from congeners except *E. communicans* Golovatch, Geoffroy, Mauriès & VandenSpiegel, 2009 by the strongly underdeveloped paraterga 2, coupled

Figure 31. *Eutrichodesmus reductus* sp. n., ♂ and ♀ paratypes; habitus, lateral view. (Photographed not to scale by L. Deharveng).

with 19 body segments and the absence of metatergal tuberculation; from *E. communicans* by a very short tergal trichome, from it and other congeners in a few minor details of gonopod structure (in particular, the shape of the telopodite).

Description: Length of adults of both sexes ca 4.0-4.2 mm, width 0.45-0.5 mm, body broadest at midbody segments. Holotype ca 4.0 mm long and 0.45 mm wide. Coloration uniformly pallid, shown pinkish because of a photographic artifact (Fig. 31).

Adults with 19 segments, body subcylindrical (Figs 31, 32A), volvation apparently incomplete due to insufficiently wide and low paraterga. Head (Fig. 33A) slightly transverse, with a poorly separated pair of very low, paramedian tubercles above antennal sockets; antennae relatively short and clavate, antennomere 6 longest; tegument (Figs 33C-E) and many other characters (Figs 32F, 33B) much as in *E. distinctus* sp. n.; collum and following metaterga devoid of tuberculation, beset with numerous, irregularly arranged, extremely short setae (Fig. 32B-F, 33C-E). Paraterga directed ventrolaterad, slightly interrupting contour of convex dorsum, short, not reaching level of venter (Figs 32A-D); paraterga 2 (Fig. 32B) only a little enlarged compared to following ones, indistinctly lobulate both anterolaterally and laterally, with only a single noticeable lobe forming a schism ledge, both schism and hyposchism very small; paraterga 3 and 4 not narrower than others, overlap typical already from paraterga 4, not paraterga 5 as in preceding congeners. Paraterga broadly rounded caudally, very indistinctly lobulate laterally

and with a single evident lobulation caudolaterally (Figs 32C-E, 33C). Limbus distinctly denticulate, almost hidden by nearby abundant microvilli (Fig. 33D, E). Pore formula normal, ozopores located dorsally near base of caudal corner of paraterga (Fig. 33C).

Legs relatively long and slender, evidently surpassing edge of paraterga (Fig. 33B).

Gonopods (Fig. 33F, G) relatively complex. Coxae abundantly micropapillate, but only with a few macrosetae. Telopodite elongate, only slightly arcuate, with a large, papillate, peculiar, distofemoral outgrowth (dp) in distal one-third and a slender but short solenomere bearing a few small setae (but no pad!) subapically at base of a very

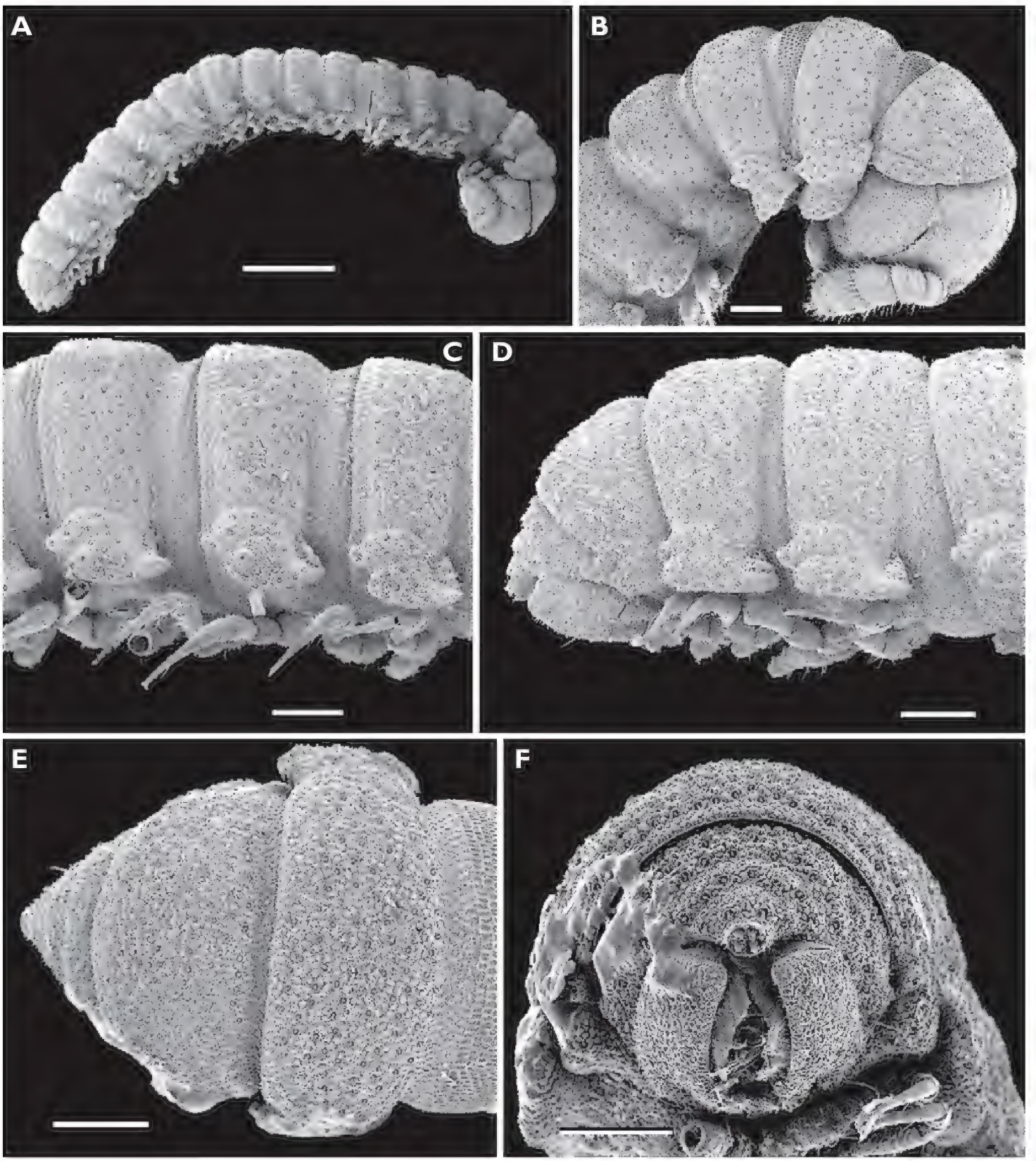


Figure 32. *Eutrichodesmus reductus* sp. n., ♀ paratype; **A**, habitus, lateral view; **B**, anterior part of body, lateral view; **C**, midbody segments, lateral view; **D-F**, posterior part of body, lateral, dorsal and caudal views, respectively. – Scale bars: A, 0.5 mm; B-F, 0.1 mm.

complex tip represented by two erect teeth, a longer uncus and a group of minute outgrowths.

Remarks: This small-bodied, pallid, non-volvatory (= "haplodesmid", see Golovatch et al. 2009) species seems to be especially close, morphologically as well as geographically, to *E. communicans* from Vanuatu, Melanesia, southwestern Pacific (Golovatch et al. 2009), possibly representing still one more troglobite.

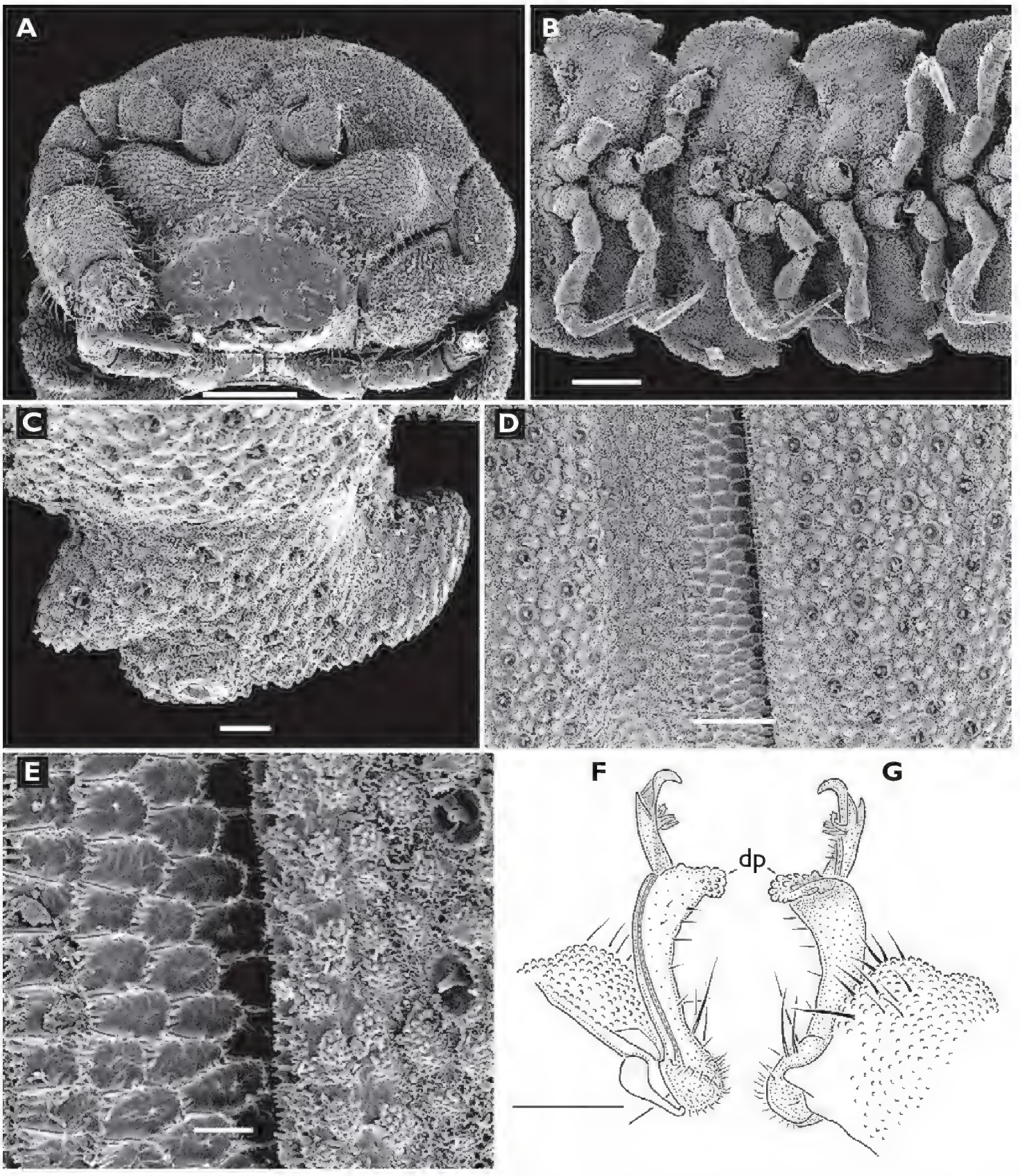


Figure 33. *Eutrichodesmus reductus* sp. n., ♀ (A-E) & ♂ (F-G) paratypes; **A**, head, ventral view; **B**, midbody segments, ventral view; **C**, midbody paratergum with ozopore, dorsal view; **D, E**, texture of tegument, dorsal view; **F, G**, left gonopod, mesal and lateral views, respectively. – Scale bars: A, B, 0.1 mm; C, 0.02 mm; D, 0.05 mm, E, 0.01 mm; F, G, 0.1 mm.

Discussion

Now that *Eutrichodesmus* has grown even more speciose, containing 24 species and no doubt with more still remaining to be discovered, it seems appropriate to redefine it and provide an updated key.

The definition of the genus (cf. Golovatch et al. 2009) is therefore amended as follows:

Eutrichodesmus Silvestri, 1910
Type-species: *Eutrichodesmus demangei* Silvestri, 1910, by original designation.

New diagnosis
Body usually "doratodesmid", with or without mid-dorsal projections; conglobation usually complete, only seldom imperfect due to underdeveloped or hypertrophied paraterga. Collum and metaterga often (micro)setose, usually tuberculate, only rarely smooth. Gonopod coxae usually abundantly setose ventrolaterally; telopodite usually slender, not enlarged towards end of femorite, but typically with a more or less distinct process or outgrowth laterally, opposite recurvature point of seminal groove; solenomere thereafter usually comprising most of telopodite, sometimes elaborate; seminal groove normally terminating distally to subapically, with or without a hairpad; acropodite normally small to nearly absent.

Key to the species of *Eutrichodesmus*

1 At least some metaterga with an evident mid-dorsal outgrowth or projection (Figs 9A-D; 20A-D)..... **2**
– All metaterga subequal, devoid of an evident mid-dorsal outgrowth or projection (Figs 2A-F, 5A-D; 17A-D)..... **9**
2 Only last 3-8 metaterga in front of telson with a very evident mid-dorsal outgrowth. Body with 20 segments..... **3**
– Most of metaterga, including some of anterior body portion, with a high, often tuberculated projection (Figs 9A-D; 20A-D). Body with 19 or 20 segments..... **5**
3 Metaterga 12-19 each with an increasingly evident, subtriangular, mid-dorsal outgrowth. Cave in Yunnan Prov., China..... ***E. dorsiangulatus***
– Only metaterga 16(17)-19 each with an evident, rather rounded, mid-dorsal outgrowth..... **4**
4 Paraterga narrower. Gonopod process dp less than one-quarter length of acropodite. North Vietnam ..... ***E. armatocaudatus***
– Paraterga broader. Gonopod process dp much longer, more than half length of acropodite. Cave in Yunnan Prov., China..... ***E. monodentus***

5 Mid-dorsal projections relatively low, not club-shaped, increasingly evident on metaterga 3–17(18) (Fig. 20A) **6**

– Mid-dorsal projections especially prominent, club-shaped, present on metaterga (4)5-19, only slightly lower on metatergum 19 7

6 Body with 19 segments. Subtriangular mid-dorsal projections evident on metaterga 3-17, only slightly smaller on metatergum 18 (Fig. 20A). Gonopod process dp rudimentary (Figs 22E, F). Vietnam ..... ***E. asteroides* sp. n.**

– Body with 20 segments. Clearly tridentate mid-dorsal projections evident on metaterga 3-18, abruptly smaller on metatergum 19. Gonopod process dp small but evident. Malaysia ..... ***E. cavernicola***

7 Metatergum 4 with a high mid-dorsal projection (Fig. 9A). Paraterga strongly declivous and quadrilobate (Figs 9A-D, 10E). Gonopods as in Fig. 11. Vietnam ..... ***E. aster* sp. n.**

– Mid-dorsal projections absent from metatergum 4. Paraterga less strongly declivous. Gonopods different. Malaysia **8**

8 Mid-dorsal projections on metaterga 5 and 6 straight in lateral view ..... ***E. macclurei***

– Mid-dorsal projections on metaterga 5 and 6 slightly inclined anteriorly in lateral view ..... ***E. reclinatus***

9 Body with 19 segments. Collum and metaterga virtually smooth, non-tuberculate, beset with long or short trichome (Fig. 32A-F, 33C-E). Paraterga too short to allow complete body volvation (Fig. 32A). Gonopod telopodite with a complex, lobiform dp (Fig. 33F, G). Southwestern Pacific **10**

– Body with 20 segments. Collum and metaterga clearly tuberculate, trichome (if present) usually short (Figs 25F, 29F). Paraterga much broader, mostly reaching level of venter, so volvation usually complete. East and Southeast Asia **11**

10 Collum and metaterga beset with long, 2-segmented, tactile setae. Tip of gonopod telopodite without teeth. Vanuatu ..... ***E. communicans***

– Collum and metaterga beset with very short trichome (Figs 32B-E, 33C-E). Tip of gonopod telopodite with a few teeth (Figs 33F, G). Sulawesi, Indonesia ..... ***E. reductus* sp. n.**

11 Paraterga mostly especially wide and only slightly declivous. Caves in Guangxi Province, China **12**

– Paraterga not so wide, strongly declivous (Figs 2A, 5A, 13A, 17A, 28A) ... **13**

12 Collum with a row of conspicuous teeth along fore edge of collum ..... ***E. similis***

– Collum with only minute teeth at fore edge of collum ..... ***E. latus***

13 Most metaterga with two transverse rows of bosses. Epiproct very strongly flattened dorsoventrally, subquadrate, spatuliform, with unincised margins. Gonopod telopodite particularly slender, about twice as long as coxa. Shikoku, Japan ..... ***E. peculiaris***

– Most metaterga with three transverse rows of bosses or conical tubercles. Epiproct never so strongly flattened. Gonopod telopodite usually shorter. Southeast Asia **14**

14 Paraterga mostly set off laterally at base by a clear sulcus. Metaterga with three mixostictic rows of evident, conical tubercles, each surmounted by a long, 2-segmented seta. Gonopod telopodite with a particularly small, dentiform dp. Thailand ..... ***E. gremialis***

– Paraterga less markedly (if at all) set off laterally at base (Figs 2A, 5A, 13A, 17A, 28A), largely continuing general outline of metaterga or nearly so (Figs 18D, 29C). Metatergal trichome very short or missing. Gonopod telopodite different **15**

15 Paraterga relatively short, volvation apparently imperfect (Fig. 24A). Body small, up to 6.5 mm long. Vietnam **16**

– Paraterga broad enough to allow complete volvation (Figs 17A, 28A). Body usually larger **17**

16 Entire body pallid, up to 5.0 mm long. Gonopods simple ..... ***E. basalis***

– Vertex, collum, metaterga and much of telson grey, this strongly contrasting with pallid venter and legs (Fig. 23). Body 6.0-6.5 mm long. Gonopods more elaborate (Figs 26C-E) ..... ***E. griseus* sp. n.**

17 Pattern of metatergal tuberculation isostictic (Figs 5A-D). Seminal groove terminating on a very evident, pilose-spiculate pulvillus near base of a relatively shortened, lamellar acropodite (Figs 6F, G, 7A-F) ..... ***E. regularis* sp. n.**

– Metatergal tuberculation mixostictic (Figs 13A-F, 24A). Seminal groove terminating distally to subapically, mostly without a pulvillus (seldom with a hairpad) (Figs 18G, H, 30) **18**

18 Distofemoral process of gonotelopodite bare, subunciform, pointed **19**

– Distofemoral process of gonotelopodite nearly always conspicuously papillate (Figs 18G, H, 30), seldom redumentary (Figs 15A-F), never pointed **20**

19 Body ca 8.0 mm long. Gonopod tip bifid. Vietnam ..... ***E. demangei***

– Body ca 14.0 mm long. Gonopod tip simple, unciform. Cave in Yunnan Prov., China ..... ***E. arcicollaris***

20 Paraterga mostly bilobate laterally and unilobate caudolaterally (Fig. 17A). Very small: 4.7-5.3 mm long and 0.65-0.7 mm wide. Gonopods as in Figs 18G, H. Vietnam ..... ***E. curticornis* sp. n.**

– Paraterga mostly 3- or 4-lobate laterally (Figs 13A-D). Length ≥ 6.0 mm, width ≥ 1.1 mm. Gonopods different **21**

21 Metaterga 18 and 19 not elevated dorsally. Caudolateral lobulations mostly deeply incised. Distofemoral process of gonopod bipartite. Caves in Guizhou Prov., China ..... ***E. incisus***

– Metaterga 18 and 19 slightly elevated dorsally (Figs 28A-F). Caudolateral lobulations not incised, tuberculiform. Distofemoral process of gonopod unipartite (Fig. 30) **22**

22 Body 6.0-6.5 mm long and 1.1-1.2 mm wide. Ozopores opening on top of porosteles representing penultimate of five lateral lobulations of respective paraterga, with caudolateral lobulations missing. Gonocoxae with only few macrosetae. Gonopods as in Fig. 30. Laos..... ***E. multilobatus* sp. n.**

– Body ≥ 8.0 mm long and 1.35 mm wide. Ozopores opening dorsally on caudalmost of 3-4 lateral lobulations of respective paraterga, caudolateral lobulations present. Gonocoxae with abundant macrosetae. Gonopods different.... ..... **23**

23 Body 8.0-8.5 mm long and 1.35-1.4 mm wide. Paraterga mostly 3-lobate (Figs 2A-G). Gonopods as in Figs 3E-H. Cave in Guizhou Prov., China..... ..... ***E. distinctus* sp. n.**

– Body 12-13 mm long and 2.5-2.6 mm wide. Paraterga mostly 4-lobate (Figs 13A-D). Gonopods as in Figs 15A-F. Caves in Thanh Hoa Prov., Vietnam... ..... ***E. filisetiger* sp. n.**

Conclusion

As stated recently (Golovatch et al. 2009), there seem to be almost no coherent patterns in the distribution of the various non-genitalic and gonopodal characters in *Eutrichodesmus*. The same concerns geographic patterns. Only a few pairs of particularly similar species can be distinguished in this speciose genus: e.g. *E. macclurei* and *E. reclinatus*, *E. latus* and *E. similis*, *E. demangei* and *E. arcicollaris*, and *E. communicans* and *E. reductus* sp. n. However, it is still too early to attempt to discriminate species groups, because many more new species of *Eutrichodesmus* can be expected to occur at least in East and Southeast Asia, as well as in the Indo-Australian archipelago, which seem to represent the centre of diversity of this genus (Fig. 34), and of the entire family Haplodesmidae.

That most of the *Eutrichodesmus* species have been found and described from cave material alone does not necessarily mean their obligate cavernicoly, even though many of them exhibit troglomorphic features. Most of the caves are simply better explored than the adjacent, much less prospected, epigean habitats.

Acknowledgements

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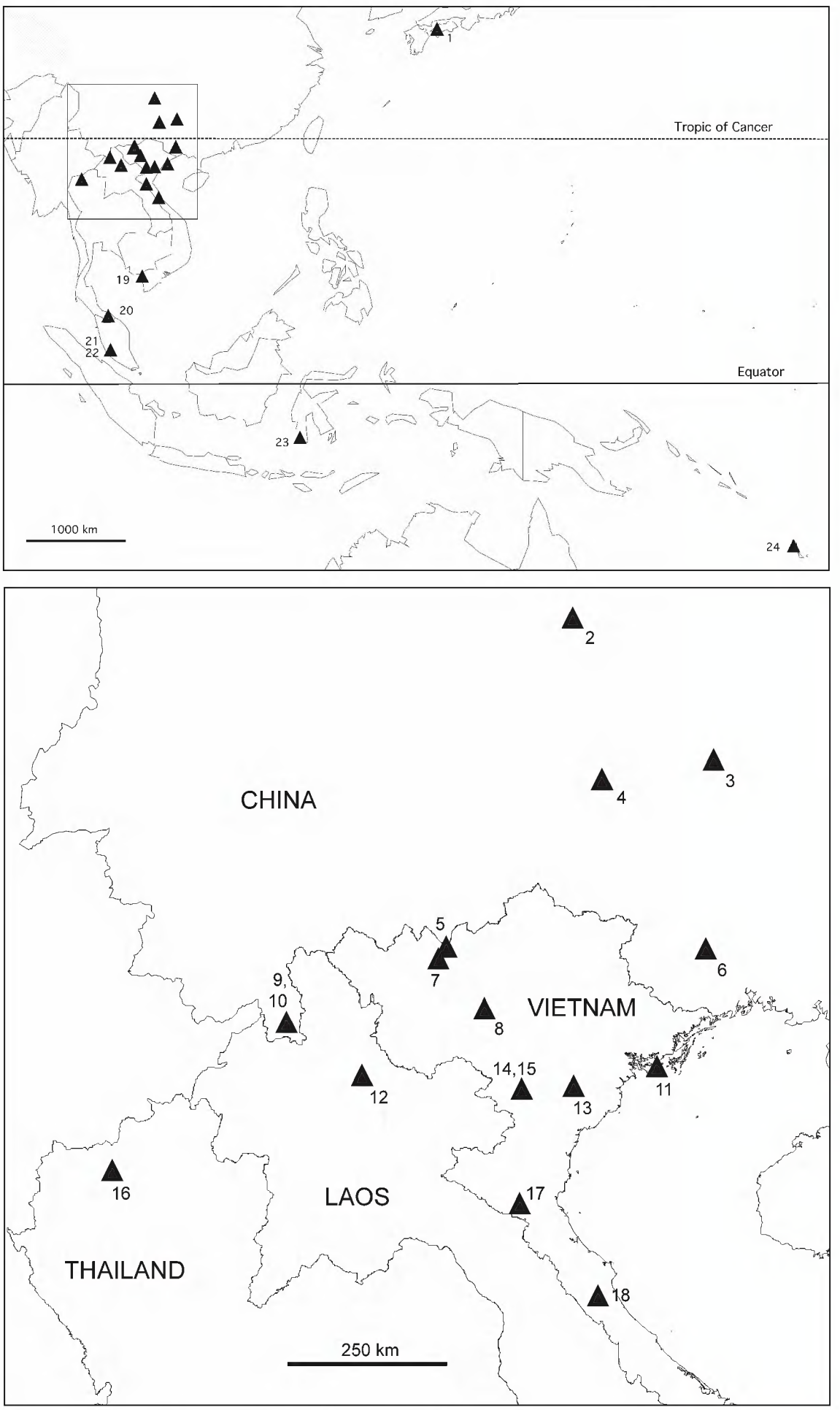

Figure 34. Map showing the general distribution of *Eutrichodesmus* species (A) and an enlarged section thereof showing the distribution of species in southern China and northern Indochina (B).
1 – *E. peculiaris*; 2 – *E. incisus*; 3 – *E. similis*; 4 – *E. latus*; 5 – *E. arcicollaris*; 6 – *E. distinctus* sp. n.; 7 – *E. regularis* sp. n.; 8 – *E. aster* sp. n.; 9 – *E. dorsiangulatus*; 10 – *E. monodentus*; 11 – *E. basalis*; 12 – *E. multilobatus* sp. n.; 13 – *E. demangei*; 14 – *E. filisetiger* sp. n.; 15 – *E. armatocaudatus*; 16 – *E. gremialis*; 17 – *E. curticornis* sp. n.; 18 – *E. asteroides* sp. n.; 19 – *E. griseus* sp. n.; 20 – *E. cavernicola*; 21 – *E. macclurei*; 22 – *E. reclinatus*; 23 – *E. reductus* sp. n.; 24 – *E. communicans*.

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